
ISBN 9789082561166

Cover photo: Pieterjan Verhelst

Printed by:

Drukkerij Lowyck
Archimedesstraat 53
8400 Oostende



Marine Biology Research Group
Campus Sterre – S8
Krijgslaan 281
9000 Gent

Academic year 2018 – 2019

Publically defended on December 7th, 2018

For citation to published work reprinted in this thesis, please refer to the original publications.

Verhelst, P. (2018). European eel (*Anguilla anguilla* L.) movement behaviour in relation to habitat fragmentation - Novel insights inferred from acoustic telemetry. Ghent University, 381pp.

GHENT UNIVERSITY

ACADEMIC YEAR 2018 - 2019

**European eel (*Anguilla anguilla* L.) movement behaviour in
relation to habitat fragmentation**

-

Novel insights inferred from acoustic telemetry

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Thesis submitted in partial fulfilment of the requirements for the degree of
Doctor in Science – Biology



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Financial and logistic support

This work was co-funded through a grant from the Flemish Agency for Innovation and Entrepreneurship (VLAIO) (now under the auspices of the National Science Fund FWO) and the Flemish contribution to LifeWatch. Part of this research was funded by De Vlaamse Waterweg nv and the Belgian Nature and Forest Agency. This work was supported by data and infrastructure provided by the Research Institute for Nature and Forest, Flanders Marine Institute (RV Simon Stevin and RHIB Zeekat), DAB VLOOT, Royal Belgian Institute of Natural Sciences (Operational Directorate Natural Environment (RHIB Tuimelaar)) and Rijkswaterstaat (The Netherlands).

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Dankwoord

De afgelopen vier jaar zijn voorbij gevlogen! Ik zie mezelf nog steeds voor de lift staan in een van de overheidsgebouwen in Brussel Noord om een IWT-project te gaan verdedigen, waarbij een druk op de knop de lift me vervolgens naar het juiste verdiep zou brengen. Ik weet nog steeds niet waarvoor ik meer stress had, die lift of het gesprek met de jury van het IWT panel...

Maar hier zijn we dan, vier jaar later en een boek op tafel, eentje over het gedrag van paling dan nog wel. Een groot deel van dit werk handelt over palingmigratie en de knelpunten die ze tegenkomen tijdens hun ongelooflijke reis naar zee. En na vier jaar zwaar gefocust te zijn, begint een mens al eens terug te blikken en uit te zoomen. Daarbij ben ik tot de vaststelling gekomen dat er opvallend veel gelijkenissen zijn tussen de zeewaartse migratie van paling en het afleggen van een doctoraat. Je begint aan een reis waar je denkt klaar voor te zijn, maar in het begin moet je meermaals even pauze nemen om de zaken toch nog eens goed te overpeinzen. Je vervolgt je weg en gelukkig is die met de stroom mee, een duwtje in de rug als het ware. Fijn, aangenaam zelfs. En dan gebeurt het, je eerste migratieknelpunt. Je botst op een muur waar je maar niet langs kan. Uren worden dagen, dagen worden weken, weken

maanden... frustraties. Maar dan is er de waterbeheerder die het knelpunt opheft waardoor je je weg verder kan zetten. Eindelijk, er is weer hoop en je kan de reis verderzetten, de zee in het achterhoofd. Onderweg is de tocht soms eindeloos; je neemt zelfs eens de verkeerde weg, waarna je moedeloos mag terugkeren om vervolgens de juiste afslag te nemen. Gelukkig kom je onderweg gelijkgestemde palingen tegen of brasems en blankvoorns die door hun entertainment de reis vanaf de zijkant aangenaam en hoopvol maken. Plots kom je in een stroomversnelling, leidend tot momenten van euforie, want het gaat plots zo gemakkelijk. Dat blijkt dan vals alarm... Meer nog, de stroomversnelling werd gegenereerd door een volgend migratieknelpunt, een pompstation. Uiteraard aarzel je om door die mixer te gaan, want dat kan toch niet goedkomen? Je stelt je de vraag hoe dit probleem best aan te pakken en gelukkig kan je hiervoor gebruik maken van het onderweg verkregen advies. Tenslotte ga je los door de pomp en aan de andere kant blijkt dat je het gehaald hebt, zij het met enkele kneuzingen, maar die genezen wel. En daar is ze dan, de zee.

Dit doctoraat is het resultaat van de bijdrage van heel wat mensen en ik denk (hoop) dat de meeste mensen zich zullen herkennen in het bovenstaande verhaal. Zij het als de stroming in de rug, de waterbeheerder, de palingen die in hetzelfde schuitje zitten of de blankvoorns en brasems die vanaf de zijlijn aanmoedigen. Ik kan gerust nog een boek schrijven over de mensen die me geholpen hebben bij het voltooien van dit werk (zelfs dikker dan den dezen), maar ik zal me jammer genoeg moeten beperken tot enkele pagina's.

Laat me beginnen met de mensen die er van bij dag één bij waren, de vier promotoren: Jan (Reubens; er passeren nog een aantal Jans), Ans, Tom en Peter.

Ik kan zonder twijfel zeggen dat we een fantastisch team waren. De frequente meetings het eerste jaar hebben me meteen op het juiste spoor gezet, waardoor ik heel efficiënt te werk kon gaan. Jullie gaven me de vrijheid om mijn eigen ding te doen, maar waren er wanneer ik voor een knelpunt stond. Dit apprecieer ik enorm! Jan, de vele uren die we gediscussieerd hebben in onze bureau waren voor mij goud waard en de meest leerrijke momenten uit mijn doctoraat. Het was tijdens deze momenten dat je me dwong om kritisch te blijven denken en bepaalde zaken eens herover te doen. Maar het belangrijkste van al is je motivatie en plezier waarmee je je werk uitvoert. Dit werkte heel aanstekelijk! Ans, ik zie ons nog altijd zitten aan de oevers van het Leopoldkanaal in de zomer van 2012, rechtover Fred's café (bij nader inzien, waarom zaten we daar niet?). Het was daar en op dat moment dat je me overtuigde om een doctoraat te doen. Ik heb de afgelopen jaren heel wat geleerd van je, mogelijks zelfs meer dan je denkt. Onze overlegmomenten waren de afgelopen jaren beperkt tot telefoongesprekken, maar daarom zeker niet minder nuttig. Tom, ik denk dat een van de eerste dingen die je tegen me gezegd hebt, op een overleg naar aanleiding van het IWT-voorstel, was "ik weet niets van vis". Uit dit doctoraat bleek dat je die kennis ook niet nodig had, gezien je veelzijdigheid en vooral je uitstekende en neutrale kijk op de conclusies die ik trok op basis van de resultaten. Je hebt gedurende het hele proces in me geloofd en stond steeds achter mijn beslissingen al dan niet met wat sturing. Ook je enorm snelle feedback op mijn mails vond ik uiterst indrukwekkend. Ik kan me nog een moment herinneren dat ik rond 01u aan het mailen was en meteen antwoord kreeg, waardoor het dan ook nog later werd. Ik denk dat we op dat moment beide iets hadden van "moet die niet slapen?". Peter, dankzij jou heb ik mijn carrière bij de Decathlon vroeger dan verwacht kunnen beëindigen om in het aquatisch beheer

terecht te komen, iets waar ik hopelijk nog lang in tewerkgesteld kan blijven. Door je betrokkenheid in buitenlandse projecten ben je niet steeds gemakkelijk te pakken te krijgen, maar je commentaren en suggesties werden steeds geapprecieerd. En een hengelsessie in het Meetjesland staat nog steeds op mijn to-do lijst.

Vervolgens wil ik ook de juryleden bedanken voor het nalezen van het doctoraat en het geven van constructieve commentaren en suggesties: Dominique Adriaens, Jan Baetens, Jan Breine, Willem Dekker en Ann Vanreusel. Ik heb genoten van de voorverdediging, opnieuw een leerrijk moment tijdens het doctoraatsproces. Dominique, bedankt voor je constructieve commentaren en het aanzetten tot grondig nadenken over de bekomen resultaten. Jan (Baetens), je kritische blik tot in het kleinste detail leidden er toe dat ik het doctoraat kon finetunen en bevestiging kreeg over de kwaliteit van het geleverde werk. Je wil om mee te denken over de statistische analyses en te zoeken naar oplossingen waardeer ik enorm. Jan (Breine), bedankt voor de lovende woorden en het vertrouwen. Ik heb met veel plezier je commentaren doorgevoerd in de finale versie. Hopelijk kunnen we in de nabije toekomst enkele methodes uit het doctoraat testen op een andere vissoort ;-)). Je bracht sfeer tijdens de voorverdediging; onmisbaar op elke verdediging naar mijn mening! Willem, net toen ik dacht dat ik de palingliteratuur kende, deelde je me je literatuurfolder van maar liefst 5 GB (!), waarin zelfs artikels uit de 18de en 19de eeuw te vinden waren, geschreven in het Duits en Frans. Je hebt de afgelopen zes weken steeds klaar gestaan om op al mijn vragen te antwoorden en me op de juiste literatuur/bron te wijzen (ik begrijp nog steeds niet hoe je alles bijhoudt; in mijn hoofd gaat het er warriger aan toe). Ann, hoofd van de Marbiol en Chairman tijdens de voorverdediging, ondanks dat jouw expertise ver van paling ligt,

heb je mijn onderzoek steeds weten te appreciëren, waarvoor dank!

Dan komen we bij de collega's. Ik zal beginnen bij de collega's van de marbiol-family. Hoewel ik vaak het gevoel had dat ik op een eiland zat wat onderzoek betreft, heb ik dit allerm minst gevoeld in sociale omgang. Ik kon me geen betere werkomgeving voorstellen en hoop dat de maandelijkse PhD-drinks blijven doorgaan! De middagpauzes waren steeds een leuke verademing, vooral de laatste maanden tijdens het schrijfwerk. Speciale dank aan Annick en Isolde om mijn bestellingen, betalingen en reservaties altijd in orde te brengen. Bedankt Marbiol! Annelien, Anna-Maria, Bart, Brecht, Bruno, Carl, Ellen P, Ellen V, Eva, Christoph, Dirk, crazy Ee Zin, Elise, Francesca, Guy, Helena, Jan V, Jens, Lara, Laurien, Liesbet, Lisa, Luana, Mohammed, Freija, Ivan, Nele, Nene, Marleen, Sebastiaan, Siel, Tania, Thibault, Thomas, Tim T, Tim V en Ulrike.

Dat brengt me bij het INBO. De eerste keer dat ik in contact kwam met onderzoek naar vis was als bachelorstudent onder de begeleiding van Ine Pauwels. Leerling volgt leraar denk ik dan. Of was het mother duckling? Samen naar congressen, symposia en de shad chat in de UK, het was machtig! De vele discussies en gesprekken hebben heel wat bijgedragen aan mijn vooropgestelde hypothesen en getrokken conclusies (bij deze, als iemand niet akkoord gaat met een van mijn conclusies, dit komt dus door het inbo). Graag wil ik hier toch even de veldwerkers in de kijker zetten. Ik heb echt dusd respect voor jullie! Jullie volbrengen het feitelijke werk in het veld; zonder jullie zijn er geen resultaten. Of het nu regent of koud is, in som super lange dagen zijn, jullie zetten je de volle 100% in. Twee mensen die ik daarbij in het bijzonder wil bedanken zijn Nico en Seb. Jullie stonden steeds paraat om me

te helpen op de Schelde om receivers te gaan uitlezen of te helpen zenderen. Zoals begin dit jaar, toen we op 31 januari naar de Zeeschelde trokken om de receivers uit te lezen. Een ganse dag op de Schelde op een bootje in de gietende regen en vrieskou! Ik denk op een bepaald moment zelfs hagel, maar het kan zijn dat ik het niet meer voelde; ik voelde dan ook praktisch niets meer in mijn handen door de kou. En als dat niet genoeg was, moesten we hier en daar nog eens door modder die tot aan de knieën kwam. Ik was nat tot op mijn ondergoed, iets wat je liever niet meemaakt medio-winter. En die gasten geven dus geen krimp! Opnieuw, duusd respect! Daarom bedankt David 'Buzios', Emilie, Ine, Jeroen, Johan, Karen, Lore, Nico, Raf, Seb en Sophie. Raf, Nico en Seb, ik hoop dat er volgend jaar opnieuw een vistrip wordt gepland ;-)? Is er ondertussen al iets geregeld om een te gaan drinken in de nieuwe Dolle Mol in Brussel? Ik heb sinds de heropening nog niet van onderbroek verandert, dus die is alvast klaar voor aan de muur!

Ook wil ik het LifeWatch team van het INBO bedanken. Stijn, Damiano en Peter, jullie hebben geen idee hoe sterk jullie bijdrage is geweest aan dit werk. Zonder R krijg ik de datasets simpelweg niet open (weetje: het maximum aantal rijen dat Excel kan genereren is 1048576), waardoor jullie programmeer kennis, bug-fixing en coding clubs onmisbaar waren. Jullie hebben me geleerd om mijn code transparant op te stellen, goed te documenteren en geordend te werk te gaan met behulp van GitHub. Dit heeft me zonder twijfel heel wat tijd uitgespaard, doordat ik de draad gemakkelijk weer kon oppikken wanneer ik een code of repo voor een lange tijd niet bekeken had. Enorm bedankt voor het actief meedenken naar methodologische oplossingen om bepaalde zaken te analyseren. Damiano, het script dat je geschreven hebt om een onderscheid te maken tussen palingmigratie en -dispersie is echt fantastisch en hoop ik toe te

passen op andere datasets om te checken hoe breed inzetbaar onze regels zijn. Stijn, het is jij die me overtuigd hebt om mijn doctoraat in LaTeX te schrijven en je hebt gelijk, machtig programma!

Naast het INBO heb ik heel wat beroep kunnen doen op het VLIZ. In eerste instantie wil ik het datacentrum bedanken. Zij hebben een database ontwikkeld waarin we niet alleen onze telemetriedata kunnen uploaden, ook stelt die in staat om onze metadata bij te houden, wat ons werk veel efficiënter en transparanter maakt. Met een netwerk van meer dan 150 receivers en een paar honderd gezenderde vissen is het namelijk niet meer eenvoudig om alles deftig bij te houden. Bedankt Benny, Filip Klaas, Tjess en Robin! Daarnaast wil ik ook nog Dre, Jan V, Tim en Wim bedanken. Ik keek steeds uit om opnieuw met jullie en de RHIB Zeekat een dagje op zee of de Westerschelde te vertoeven om receivers te gaan uitlezen. Ook de bemanning van de RV Simon Stevin wil ik langs deze weg bedanken voor de vele expedities op zee om receivers uit te lezen en gulletjes te gaan zenderen.

In 2016 kreeg ik de unieke kans om samen met het communicatieteam van het VLIZ een animatiefilmpje te ontwikkelen rond het telemetrieonderzoek op paling. Hiervoor hebben we samen gewerkt met animator Steve Bridger die uitstekend werk heeft verricht en die indrukwekkend snel mijn gedachtegang kon volgen (ik kan het zelf zo snel niet!). En als dat nog niet genoeg was, hebben we een persbericht losgelaten bij release van het animatiefilmpje, wat heel goed ontvangen werd door de media. Jan (Seys), als jij me niet zo goed had voorbereid op wat en vooral hoe ik moest antwoorden op de vragen door interviewers, ging dit niet goed gekomen zijn! Bedankt communicatieteam en in het bijzonder Jan en Karen!

Ondanks dat we als een parafyletische groep beschouwd kunnen worden, vormen we een hecht team: team telemetry! Zoals elke groep zijn we klein begonnen, maar hij groeit gestaag. Ik denk dat een van onze pluspunten is dat we elkaar versterken: we leren van elkaar, maar blijven ook kritisch voor elkaar. Ik hoop dat we samen nog enkele telemetrie congressen mogen meemaken. De laatste was alleszins eentje om niet te vergeten, evenals de vele workshops. Bedankt Ine, Inge, Jan, Jenna, Jolien en Stijn!

Hoewel het op een dood spoor is uitgedraaid, heb ik er zeker geen spijt van om een telemetrienetwerk in het Verdrongen Land van Saeftinghe op te stellen. Jammer dat we maar 1 paling te pakken kregen, een reden waarnaar ik nu nog af en toe zoek... Het was de bewuste zomer van 2016 dat ik een 6 tal weken in het gebied vertoeft heb, met strandkar, waadpak, bakken en netten om het gedrag van paling in een slikken en schorrensysteem te bestuderen. Enige wat ik er aan overgehouden heb zijn twee littekens op mijn kuit (kruip nooit, maar dan ook nooit in een short in een waadpak!). Of nee, ik zou liegen, ik heb daar een fantastische zomer beleefd met gidsen Marc en Bas langs mijn zij om het materiaal te helpen rondzeulen en me heel wat bij te brengen over de flora en fauna van het gebied. In het bezoekerscentrum werd ik steeds verwelkomd door Carla of Pepijn met verse koffie. Het veldwerk werd vaak afgesloten in het café "Het Verdrongen Land", waar de boerenzwaluwen binnen en buiten vliegen en er foto's van blote madammen op de tafels staan. Wat wilt een mens nog meer.

Binnen het academische wil ik graag nog de studenten bedanken die hebben meegeholpen aan dit project. Ik vond het zeker geen evidentie om jullie te begeleiden en hoop dat jullie er dezelfde voldoening uit gehaald hebben als

ik. Bedankt Charlotte, Joachim, Jolien, Lisann, Lore, Michiel, Natacha, Rutger, Sam, Thomas en Toon.

Aan de bio-vrienden, het is alweer uitkijken naar het volgende bioweekend in februari. Een wintereditie, jenever mag niet ontbreken denk ik dan. Rik, het weekendje Houffalize kwam net op tijd: ik zat toen midden ‘in the zone’ van het schrijven en een weekendje vissen gecombineerd met wildlife spotting heeft daar goed aan gedaan. Jens, de regelmatige cinematrips lieten me ook goed ontspannen. En het voorafgaande bezoek aan de frituur of pizzeria, verteren. We plannen een dezer eens een cinema-avondje, want moet nog wat schade inhalen. Langs deze weg, merci An-Sofie, Catherine, Emma, Jorunn, Koen, Silke, Maxime, Mick, Rieneke, Tim, Timothy en Yana.

Vervolgens wil ik ook de mensen rond het Kortrijkse bedanken. Merci Dobby, Gre, Tom, Tijs, Jerre enno! Ook de vrienden van rond Wevelgem: Brian, Karl, Lana, Lore, Michael en Sanne. En natuurlijk de Izegemners Lore en Sander. Als jullie nog eens vragen hebben over paling, je moet dit boek maar eens lezen. Of vragen mag natuurlijk ook.

Verder wil ik de vrienden van het vissen bedanken. Tom, Danny, Francis en heel de bende, het is tijdens momenten aan het water dat ik mijn werk kon loslaten en mijn focus op iets anders kon zetten. Dat begint echter ook al aardig te lukken als ik eens vogels ga spotten. Wouter, 16de staat dus vast é!

Mijn zus, familie, schoonfamilie, Fluppe en Marleen wil ik bedanken voor de constante steun en geïnteresseerde vragen over paling (hoewel, sommige gingen nogal eens over gerechten en paling kweken...). Bedankt voor de leuke familiemomenten, Bourgondische maaltijden en het altijd klaarstaan voor hulp bij karweien in en rond het huis.

Ma, pa, ik weet niet goed hoe ik jullie moet bedanken, want dat is niet met woorden uit te drukken. De kansen die ik in mijn leven gekregen heb door jullie, heb ik zoveel mogelijk proberen grijpen. Bedankt voor de onvoorwaardelijke liefde, het vertrouwen en bovenal, het warme nest in Snellegem!

Lieselot, Hotty Lotty, vroeger Lotty, nu meestal de Lotn. Je bent de enige in heel dit verhaal die het van zo dichtbij heeft gevolgd. Hoe je het hebt uitgehouden, is mij nog steeds een raadsel, maar duizendmaal dank om mij er niet uit te gooien, wanneer ik het voor de zoveelste keer over paling had of een analyse die maar niet wilde lukken. Je hebt de ups en downs meegemaakt en wist me steeds weer boven water te halen, wanneer ik verdronk in het werk. Ik heb het je nooit gezegd, maar je streven naar efficiëntie is iets wat ik heb proberen kopiëren. Er zijn talloze situaties geweest waarin ik je in mijn hoofd hoorde zeggen “how Pietje, das nie efficiënt, doe da ki anders”. Het is me in veel situaties gelukt (denk ik), maar dat bellen is toch niet mijn ding. Super dikke merci voor de steun, feedback en om gewoon jou te zijn!

Ik ben mijn verhaal gestopt wanneer de paling de zee bereikte, maar daarmee is haar reis nog niet voltooid. Het langste deel van de tocht ligt nog voor haar: duizenden kilometers door de oceaan met sterke stromingen, roofdieren, vissers en mogelijks nog heel wat zaken waarvan we de impact niet kennen. Het leven stopt niet bij 1 uitdaging, er gaan er nog veel volgen en het zijn deze uitdagingen die ons onze grenzen doen verleggen.

Summary

An ever increasing human population has led to global change, resulting in substantial pressures on ecosystems and diversity loss by (in general) acting on five fronts: (a) climate change, (b) habitat modifications resulting in habitat loss and fragmentation, (c) biogeochemical and hydrological cycles and pollution, (d) biological invasions, and (e) overexploitation of natural resources. Consequently, maintaining species diversity and ecosystem functioning will increasingly require human intervention by adequate management. Aquatic environments are among the most anthropogenically altered systems. Impact often results in changed hydrological conditions due to land reclamation, agricultural drainage, shipping accompanied with shipping locks, construction of pumping stations, dams and weirs, waste water treatment and hydropower. Obviously this affects aquatic life.

A flagship fish species affected by global change, is the European eel (*Anguilla anguilla* L.). Its spawning grounds are assumed to be in the Sargasso Sea, after which the leptocephalus larvae drift with the Gulf Stream to continental Europe and metamorphose into glass eels. It is this stage which settles in coastal, estuarine and freshwater habitats to grow as yellow eels. Once they

reached a certain size and accumulated enough fat, they migrate back to the spawning site as silver eels. Yet, over the last four decades, their glass eel recruitment numbers have plummeted by 90 – 99%, leading to the 'critically endangered' IUCN Red List status. This worrisome decline resulted in the adoption of the EU Eel Regulation in 2007 which states that European countries need to take management measures to ensure 40% escapement of the spawning stock biomass, defined as the best estimate of the theoretical escapement rate if the stock were completely free of anthropogenic influences. However, as all five components of global change affect the European eel population, taking effective measures is not straightforward. Currently, management mainly focuses on fisheries regulation and redistribution of glass eels from high abundance to low abundance areas. Yet, effectiveness of these actions is questionable as long as climate change, habitat quality and connectivity, pollution and biological invasions are not addressed. To include those aspects in eel management, a better understanding is required. Consequently, to partly cover this knowledge gap, habitat quality and connectivity were the central focus of this dissertation. Connectivity between freshwater habitats and marine areas is heavily obstructed by anthropogenic structures (e.g. weirs, pumping stations, shipping locks, sluices...), leading to a high pressure on the European eel population. A better understanding of fish migration behaviour in relation to these barriers is needed to take proper mitigation actions. To understand eels' habitat use, we applied acoustic telemetry to reveal their movement behaviour in various aquatic systems and habitat types. Acoustic telemetry involves acoustically tagged animals which can be detected by a network of acoustic listening stations.

In chapter three, we investigated the movement behaviour of large female

yellow eels in a polder area, characterized by interconnected canals, polder ditches and ponds. The study illustrated that yellow eels have a high site fidelity and that their movement is not strongly affected by environmental factors (temperature, precipitation, day length, atmospheric pressure, pumping discharge). This may be attributed to their opportunistic behaviour and productivity of the polder system, which makes such systems highly suitable as eel growth habitats. In view of their high site fidelity, large female yellow eels may not encounter many human-induced connectivity problems in polder systems. In addition, our study indicated that large eels prefer deeper habitats. If measures concerning eel habitat restoration in polders are considered, areas of sufficient depth need to be maintained for large eels. A higher yellow eel survival could in turn result in a higher silver eel escapement, and as such could help meet the 40% escapement obligation imposed by the European Eel Regulation.

In accordance with eels' opportunistic feeding behaviour, chapter four handles head width distribution of eels in the Schelde Estuary. As eels are opportunistic feeders, it is doubtful that head width follows a bimodal distribution with the dichotomous characterization of narrow and broad headed specimens. Indeed, our study showed a continuum of narrow to broad with a unimodal distribution. This pattern could illustrate there is no resource selectivity and consequently no disruptive selection for the eels in the Schelde Estuary.

In chapter five, the spatio-temporal silver eel migration behaviour was studied in a barrier-free system, i.e. the Schelde Estuary. The results of this study demonstrated that silver European eels use selective tidal stream trans-

port and underlines the importance of tides in eel migration. Hence, eels can make a distinction between ebbing and flooding tide, indicating that cues other than currents play a role in orientation. Apparently, tides help eels to migrate in a bioenergetically efficient way through estuaries, just like for other diadromous fish species such as salmonids and flounder. Therefore, restoration of estuaries, for example via tidal barrier management, may not only aid recovery of the European eel population, but of diadromous fish species in general.

The next two chapters relate to spatio-temporal silver eel migration behaviour in anthropogenically regulated systems. Regulated waterways come in various forms depending on anthropogenic needs (agricultural drainage, transport, waste water...) and accompanied migration barriers. Chapter six handles about silver eel migration behaviour in a polder system. A polder system has a lower water level than the sea and consequently needs to be drained by a pumping station to prevent it from flooding. Accompanied with a pumping station is a weir and both act as migration barriers. In chapter seven we studied a shipping canal, i.e. the Albert Canal, which is characterized by shipping locks, turbine stations and tidal sluices. Both studies showed that migration was highly hampered by the various types of migration barriers, leading to significant delays and exploratory behaviour near the barriers. In addition, the substantial low migration speeds in the canal sections of the Albert canal are likely a consequence of the highly regulated water flow, preventing a unidirectional cue for the eels to orient towards the sea. Delays can have a serious impact on eels since their energy resources are limited for a successful trans-Atlantic migration. In addition, delays and exploratory behaviour can also increase predation and disease risk. The results indicated that adequate management measures need to be taken to make migration barriers

passable and stimulate a substantial unidirectional water flow as eels are likely depending on this for orientation. As this can be economically challenging, management could act during specific migration windows when it is likely the majority of the eels are migrating. In general silver eel migration occurs from August till December at night during moments of increased precipitation and consequently increased flow.

Although these studies were conducted on a small geographical scale relative to the wide distribution of the European eel, management at different geographical locations may have substantial various outcomes on the population. In chapter eight we describe a new migration route which at least a part of the eels take to leave the North Sea. Different migration routes may have different bio-energetic implications as some routes may be energetically more demanding, leaving less energy for spawning. Consequently, local management may have an important impact on the population. However, we do not have enough information yet to determine whether something significant is happening during marine migration and whether the inland management actions taken are effective.

In this dissertation, we illustrated that migration barriers such as weirs, pumping stations, shipping locks and tidal sluices substantially hamper silver eel migration via delays, disorientation and exploratory behaviour. Therefore, adequate management measures such as fish friendly screws or gravitational flow stimulation during specific migration windows need to be taken to aid recovery of the European eel population. Yet, such management demands a constructive cooperation between ecologists and engineers. Not only the European eel, but other diadromous and potamodromous fish species will

benefit from this as well.

Samenvatting

De toenemende wereldbevolking heeft geleid tot wereldwijde veranderingen (i.e. global change), wat heeft geresulteerd in substantiële effecten op ecosystemen en verlies in diversiteit. Deze anthropogene effecten worden onderverdeeld in vijf componenten: (a) klimaatsverandering, (b) veranderingen in habitat leidend tot habitatverlies en -fragmentatie, (c) biogeochemische en hydrologische cycli, (d) introductie van invasieve soorten en (e) overexploitatie van natuurlijke bronnen. Bijgevolg zal soortbehoud en het correct functioneren van ecosystemen steeds meer menselijke inmenging vragen door doelmatig beheer. Aquatische systemen behoren tot de meest menselijk-beïnvloede systemen. Menselijke impact leidt vaak tot veranderingen in hydrologische condities door landwinning, drainage, scheepvaart, constructie van sluizen, pompstations and dammen, afvalwater en waterkracht. Het is vanzelfsprekend dat dergelijke zaken een impact hebben op het aquatisch milieu.

Een soort die sterk wordt beïnvloed door global change, is de Europese paling (*Anguilla anguilla* L.). Er wordt aangenomen dat het voortplantingsgebied zich ergens in de Sargasso Zee situeert, waarna de leptocephalus larven met de Golfstroom richting het Europese continent driften en vervolgens me-

tamorfoserende tot glasalen. Glasalen settelen zich in estuariene kustgebieden en zoetwaterhabitats om tot gele palingen te ontwikkelen. Eens ze een bepaalde grootte hebben bereikt en genoeg vet hebben geaccumuleerd, start de zeewaartse migratie richting het voortplantingsgebied als zilverpalingen. Echter, de glasaalrecrutering is de afgelopen vier decennia met 90 – 99% achteruit gegaan, wat heeft geleid tot de ‘ernstig bedreigde’ status volgens de Rode Lijst van de IUCN. Deze achteruitgang leidde tot de Europese Palingverordening in 2007. Die stelt dat Europese lidstaten acties moeten ondernemen om 40% van de uittrekkende zilverpalingen te garanderen. Deze 40% wordt beschouwd als het theoretisch uittrekkende aantal indien de populatie gevrijwaard zou zijn van antropogene activiteiten. Echter, aangezien alle vijf componenten van global change een invloed uitoefenen op de palingpopulatie, is het uitvoeren van effectieve beheersmaatregelen niet evident. Tegenwoordig wordt dit beheer voornamelijk gevoerd op het niveau van visserij en het uitzetten van glasaal, afkomstig van gebieden met relatief hoge dichtheid naar gebieden met lage dichtheid. Echter, de effectiviteit van deze maatregelen is betwistbaar zolang klimaatverandering, habitatkwaliteit en connectiviteit, vervuiling en de introductie van invasieve soorten niet in acht worden genomen. Om deze zaken in het palingbeheer op te nemen, moeten we ze beter begrijpen. Teneinde een deel van deze kennisleemte in te vullen, werden habitatkwaliteit en connectiviteit centraal naar voor geschoven in dit proefschrift. De connectiviteit tussen zoetwater en mariene habitats, en bijgevolg de Europese palingpopulatie, staat tegenwoordig zwaar onder druk door de constructie van antropogene structuren (e.g. stuwen, pompstations, sluizen...). Een betere kennis over vismigratie in relatie tot deze barrières is daarom noodzakelijk om tot een doeltreffend beheer te komen. Om het habitatgebruik te onderzoeken, maakten we gebruik

van akoestische telemetrie. Akoestische telemetrie houdt in dat dieren voorzien worden van een akoestische zender, die gedetecteerd kan worden door een netwerk van ontvangststations.

In hoofdstuk drie wordt het bewegingsgedrag onderzocht van grote vrouwelijke gele palingen in een polder gebied, gekenmerkt door kanalen, polderwaterlopen en kreken die met elkaar in verbinding staan. De studie toonde aan dat gele paling een hoge plaatsgetrouwheid heeft en dat hun bewegingspatronen niet sterk afhankelijk zijn van omgevingsvariabelen (watertemperatuur, neerslag, daglengte, luchtdruk en debiet). Dit kan te wijten zijn aan het opportunistisch gedrag van paling en de productiviteit van het poldersysteem, wat dergelijke systemen uitstekend opgroeihabitat voor paling maakt. Doordat de palingen een hoge plaatsgetrouwheid hebben, worden ze mogelijk minder gehinderd door anthropogene connectiviteitsproblemen in polders. Verder toonde de studie aan dat grote palingen relatief diep habitat prefereerden. Dus als maatregelen genomen moeten worden, ten gunste van de palingpopulatie, is het belangrijk om habitat te creëren dat voldoende diep is. Een hogere overlevingskans van gele paling kan bijgevolg resulteren in een hoger aantal migrerende zilverpalingen, waardoor deels tegemoet gekomen wordt aan de 40% ontsnappingsregel van de Europese Palingverordening.

In lijn met het opportunistisch foerageergedrag van paling, handelt hoofdstuk 4 over de distributie van de kopbreedte van paling in het Schelde-estuarium. Door het opportunistisch gedrag, is het twijfelachtig of de kopbreedte een bimodale distributie volgt, zoals vaak aangenomen wordt. Het is namelijk zo dat palingen in twee groepen worden onderverdeeld: smal- en breedkoppen. Onze studie toonde aan dat de distributie een continuum

vormde van palingen met een smalle kop naar palingen met een brede kop. Dit patroon verklaart mogelijks dat er geen selectiviteit voor voedsel optreedt en bijgevolg geen disruptieve selectie voor palingen in het Schelde-estuarium.

In hoofdstuk vijf werd het spatio-temporeel migratiegedrag van zilverpaling in een systeem zonder migratiebarrières onderzocht, i.e. het Schelde-estuarium. De resultaten van de studie toonden aan dat zilverpaling gebruik maakt van selectief getijdetransport, wat het belang van getijden in paling-migratie benadrukt. Dit gedrag veronderstelt dat palingen een onderscheid kunnen maken tussen eb en vloed, wat erop wijst dat andere factoren dan stroming een rol spelen in oriëntatie. Het toepassen van selectief getijdetransport laat de palingen toe om op een bio-energetisch efficiënte manier doorheen het estuarium te migreren, iets wat reeds werd aangetoond voor andere diadrome vissoorten zoals salmoniden en bot. Bijgevolg zal het herstel van estuaria, bijvoorbeeld door aangepast spuibeheer, niet enkel voordelig zijn voor de paling-populatie, maar voor diadrome vissoorten in het algemeen.

De volgende twee hoofdstukken handelen over het spatio-temporeel migratiegedrag van zilverpaling in een anthropogeen gereguleerd systeem. Gereguleerde waterlopen bestaan in uiteenlopende vormen, afhankelijk van de noden (drainage van landbouwgebied, transport, afvalwater...) en daarmee gelinkte migratiebarrières. Hoofdstuk zes handelt specifiek over zilverpaling migratie in een polder. Een polder wordt gekenmerkt door een waterniveau dat lager ligt dan het omringende gebied of de zee. Bijgevolg is het nodig om een polder te draineren via een pompstation om te voorkomen dat het gebied overstroomt. Naast het pompstation is in het gebied ook een stuw aanwezig en beide constructies vormen een migratiebarrière voor diadrome vissoorten.

In hoofdstuk zeven wordt een scheepvaartkanaal onderzocht, i.e. het Albertkanaal. Dit kanaal wordt gekenmerkt door sluizen voor de scheepvaart, tidale sluizen en turbine stations. Beide studies toonden aan dat migratie bemoeilijkt werd door de verschillende types migratiebarrières, wat leidde tot significante vertragingen en zoekgedrag nabij de barrières. Meer nog, de substantieel lage migratiesnelheden in de verschillende kanaalsecties van het Albertkanaal zijn waarschijnlijk te wijten aan de sterk gereguleerde doorstroming van het kanaal. Dit houdt in dat een unidirectionele stroom ontbreekt, wat een belangrijke factor is in de oriëntatie van zilverpalingen die naar zee migreren. Vertragingen kunnen een serieuze impact hebben op paling omdat hun energievoorraad nodig is voor de trans-Atlantische migratie. Ook kunnen vertragingen en zoekgedrag leiden tot een hoger risico op predatie en ziekte. Deze resultaten duiden dus op het belang van een doeltreffend beheer om migratiebarrières passeerbaar te maken enerzijds en het stimuleren van een substantiële unidirectionele doorstroming anderzijds. Omdat dergelijke maatregelen echter economisch uitdagend kunnen zijn, kan het beheer er naar streven om acties te ondernemen tijdens specifieke migratieperiodes wanneer de kans groter is dat een aanzienlijk deel van de palingen migreren. Over het algemeen vindt de palingmigratie in Europa plaats van augustus tot december tijdens momenten van verhoogde neerslag en bijgevolg afvoer.

Hoewel deze studies werden uitgevoerd op een relatief kleine geografische schaal ten opzichte van het totale verspreidingsgebied van Europese paling, kan beheer op verschillende geografische locaties substantiële effecten hebben op de populatie. In hoofdstuk acht beschrijven we een nieuwe migratieroute die door op zijn minst een deel van de zilverpalingen genomen wordt om de Noordzee te verlaten. Verschillende migratieroutes hebben mogelijks verschil-

lende bio-energetische implicaties daar sommige routes energetisch ongunstiger zijn en bijgevolg minder energie voor het paaien zelf overblijft. Bijgevolg kan lokaal beheer een belangrijke impact hebben op de populatie. Echter, om dergelijke uitspraken hard te maken, hebben we nog niet genoeg informatie over het migratiegedrag in zee en of het beheer in het zoete water effectief is.

In dit proefschrift werd aangetoond dat migratiebarrières zoals stuwen, pompstations en sluizen een substantiele impact hebben op zilverpalingmigratie en leiden tot vertragingen, desoriëntatie en zoekgedrag. Daarom dringt een doeltreffend beheer zich op om visvriendelijke vijzels te ontwikkelen of gravitaire afvoer te stimuleren tijdens migratieperiodes ten einde de palingpopulatie te herstellen. Echter, dergelijk beheer vraagt een constructieve samenwerking tussen ecologen en ingenieurs. Niet alleen de paling, maar ook andere diadrome en potamodrome vissoorten zullen baat hebben bij dergelijke acties.

List of abbreviations

AC	Albert Canal
AIC	Akaike Information Criterion
ALS	acoustic listening station
ANOVA	analysis of variance
APS	Archimedes pumping station
ATN	Animal Telemetry Network
BARN	Belgian acoustic receiver network
BIC	Bayesian Information Criterion
BPNS	Belgian part of the North Sea
BW	body weight
CPDI	close-proximity detection interference
CRAN	Comprehensive R Archive Network
ED_h	horizontal eye diameter
ED_v	vertical eye diameter
ESFRI	European Strategy Forum on Research Infrastructure
ETN	European tracking network
FL	pectoral fin length

GBIF	Global Biodiversity Information Facility
GLMM	generalized linear mixed model
GLS model	generalized least squares model
HL	head length
HW	head width
IMOS	Integrated Marine Observing System
INBO	Instituut voor Natuur en Bosonderzoek
IUCN	International Union for Conservation of Nature
KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen
LC	Leopold Canal
MGR	Minimum Gap Runner
OBIS	Ocean Biogeographic Information System
OTN	Ocean tracking network
PBARN	passive Belgian acoustic receiver network
PIT	passive integrated transponder
PSAT	pop-up satellite archival tag
RF	Random Forests
SE	Schelde Estuary
SD	standard deviation
SNR	signal-to-noise ratio
STST	selective tidal stream transport
TL	total length
VLIZ	Vlaams Instituut voor de zee
VLH turbine	very low head turbine
VUE	Vemco User Environment
W	body weight

WS	Westerschelde
ZINB model	zero-inflated negative binomial model
ZS	Zeeschelde

List of R packages

adehabitatLT	Tools for the analysis of animal movements.
blmeco	Functions accompanying Korner-Nievergelt et al. (2015).
dplyr	A set of tools for data handling and formatting.
igraph	Routines for simple graphs and network analysis.
lme4	Tools to fit linear and generalized linear mixed-effects models.
lmerTest	Provides summary tables for lmer model fits.
lubridate	Functions to work with date-times and time-spans.
nlme	Fit and compare linear and nonlinear mixed-effects models.
plyr	A set of tools for data handling and formatting.
pscl	Maximum likelihood estimation of zero-inflated models.
pwr	Power analysis functions along the lines of (Cohen, 1988).
randomForest	Classification and regression based on a forest of trees.

Chapter 1

General introduction

1.1 Connectivity and migration

Living in an anthropogenic world with an estimated population increase to 9 billion by 2050, consequences for all ecosystems on Earth are obvious (Vitousek et al., 1997). It is now widely accepted that global change results in the rapid decline or even extinction of various species on the one hand and in the (human-induced) expansion of others (Brook et al., 2008; Pimm et al., 2006). Consequently, maintaining the diversity of species and functioning of ecosystems will increasingly require human intervention. An important aspect to be addressed related to global change, diversity conservation and consequently ecosystem functioning, is habitat connectivity, allowing animal movement over convenient distances (Council, 2000). Knowledge about movement patterns is crucial for our understanding of the ecology, life history, be-

haviour and conservation of animals. Animal movement is the general term for an organism's displacement, motivated by an inherent mechanism such as feeding, resting or reproduction. Depending on that goal, animal movement can be classified in three general groups:

1. **Station keeping** is the movement of an organism within a home range towards or away from a specific location for foraging and predator avoidance (i.e. homing location such as a den or nest) (Dingle, 1996).
2. **Ranging** is the permanent movement of an organism from one home range to another (Dingle and Drake, 2007).
3. **Migration** is a persistent and unidirectional movement, characterised by the temporal inhibition of stationary responses (Kennedy, 1985).

The most extensive animal movements relate to migration, present throughout the entire animal kingdom. During the last century, many migrating animals have disappeared or declined in numbers substantially due to various anthropogenic causes with the most prominent being overexploitation, climate change, habitat destruction and migration barriers (Wilcove and Wikelski, 2008). One of the best known examples of migratory animal extinction is that of passenger pigeons (*Ectopistes migratorius* L.), a migratory bird gone extinct in 1914. The passenger pigeon was one of the most abundant endemic bird species to North-America, but due to hunting and trapping, their number declined below a sustainable population, driving them to extinction (Bucher, 1992; Halliday, 1980). A similar story holds true for the American bison (*Bison bison* L.) (Taylor, 2011): the North American population of ca. 30

million bison was decimated to nearly 100 specimens by the late 19th century to fulfill the industrial leather demand.

Further, climate change is already impacting species distributions as their niche is shifting over latitude, likely leading to alterations in community interactions (Perry et al., 2005). However, redistribution as a response to climate change of species with slow dispersal capacities, low fecundity and fragmented ranges will likely fail due to the fast pace of climate change (Aitken et al., 2008; Pearson, 2006; Thomas et al., 2004).

Finally, urbanization, roads and artificial waterways lead to habitat destruction, migration barriers and consequently a patchy habitat distribution. For example, the common toad (*Bufo bufo* L.) is the amphibian with the highest road mortality rate in Europe, attributed to its reproduction migration from wintering sites to nearby located ponds (Santos et al., 2007). Also many fish species suffer from migration barriers such as weirs, dams, pumps and hydropower stations which prevent them from successfully completing their life cycle, by impairing movement between, for instance, spawning and foraging habitats (see further) (Larinier, 2001). However, in some occasions migration barriers can act beneficial, for instance towards species rehabilitation. Specifically, migration barriers can prevent mixing of locally adapted subpopulations with introduced specimens of subpopulations from other regions or even escaped cultivated species. Especially for fish, a lot of historical stocking has been conducted for angling and rehabilitation purposes. Yet, the stocked fish often come from catchments different than the rehabilitated population. Despite sometimes impressive restocking numbers, rarely do the fish contribute to the rehabilitation process (Koskinen et al., 2002; Poteaux et al., 1998). This is

likely explained by stocked species' different genetic lineage and consequently they are not fully adapted to the local conditions, causing them being outcompeted by the local population (Fleming et al., 2000; Hansen et al., 2000). As such, Van Houdt et al. (2005) found evidence of genetic pure lineages in brown trout (*Salmo trutta* L.) in the Meuse catchment in Belgium, likely attributed to migration barriers preventing mixing with stocked specimens down river. Specimens with a pure genetic lineage can aid restoration of populations elsewhere in the river catchment. Also, migration barriers prevent the spread of invasive species. In southern California, for instance, the invasive red swamp crayfish (*Procambarus clarkii* Girard) was almost absent upstream of large barriers, while capture-recapture indicated they moved frequently between pools downstream of the barriers, illustrating their high mobility (Kerby et al., 2005).

Declining numbers of migratory species can have important consequences for ecosystems. Specifically, migrating animals play an important role in nutrient distribution. Many salmon and trout species grow to adulthood in marine environments and migrate up rivers for spawning to subsequently die. This results in a nutrient flux of marine nutrients into inland ecosystems (Wilcove and Wikelski, 2008). Due to migration barriers, salmon and trout populations in the Pacific have declined tremendously, leading to a depletion in marine nitrogen and phosphorous reception of over 90% in Northwest Pacific rivers (Gresh et al., 2000). Spring migration of song birds from Central America to Northern America had a substantial impact on insect abundance, eating over 10 tons of insects per day (Wilcove and Wikelski, 2008). Not only does this illustrate pest control, but the birds may have an important impact on nutrient distribution as well. However, nutrient distribution attributed to migration is not always positive. Large numbers of Lesser Snow Geese (*Chen caerulescens*

caerulescens L.) and Ross' Geese (*Chen rossii* Cassin) forage in nutrient rich agricultural areas, but roost in wetlands, causing a substantial nitrogen and phosphorous load in the water (Post et al., 1998). This problem arises especially due to wetlands becoming more scarcer, resulting in overcrowded space use by the geese.

Another important aspect to address related to migration, is disease spread. Many migrating animals carry zoonotic diseases (Altizer et al., 2011; Webster et al., 2002) and due to human population expansion, we interfere more frequently with those animals, leading to a higher chance of getting infected (e.g. the paramyxoviruses 'Nipah' and 'Hendra' in flying foxes (Daszak et al., 2006; Philbey et al., 1998; Plowright et al., 2008), Lyme and West-Nile virus in birds (Alekseev et al., 2001; Rappole et al., 2000) and SARS (Severe Acute Respiratory Syndrome) in carnivores (Bell et al., 2004)). Even more, by restricting animal movement, they are forced in smaller habitats and consequently occur in larger densities, which makes them more prone to diseases (Altizer et al., 2011). Salmon farms for example are susceptible to sea lice (*Lepeophtheirus salmonis* Krøyer) infections and by placing them along migration corridors, the parasite can rapidly spread across the wild population (Krkošek et al., 2007).

Despite our anthropogenic world hampers animal movement, migration in particular, a paradox exists: never before has the distribution of alien species be so prominent as during the last decades. Especially the increase of international trade, accompanied with the construction of (rail)roads and canals during the Industrial Revolution in the 1800s enhanced biological invasions (Hulme, 2009). Alien species that become invasive can pose serious economic and ecological consequences (Andersen et al., 2004; Kolar and Lodge, 2001).

They can cause shifts in ecological communities (Andersen et al., 2004; McKinney and Lockwood, 1999), thereby affecting ecosystem structure and functioning. By competing with native species, they can severely affect the density of different species within a certain ecosystem, resulting in environmental and economic costs (Pimentel et al., 2005).

1.2 Regulated water ways throughout the world and their impact on fish populations

Among the most anthropogenically altered ecosystems, are aquatic environments: worldwide, water levels of freshwater systems are controlled by structures such as pumping and hydropower stations, weirs, dams, shipping locks and sluices (Arlinghaus et al., 2002; Baumgartner et al., 2009; Bowen et al., 2003; Buysse et al., 2014; Lassalle et al., 2009). Due to global change (e.g. population increase with accompanied consumption) and climate change in particular, hydrology will be affected in the future. It has already been shown that timing of water runoff in large European catchments (e.g. Rhine, Rhône and Danube) will change by an intensifying winter and reduced summer runoff. Obviously, this will affect our hydrological management, such as navigation and hydropower developments (Schröter et al., 2005).

The above mentioned structures for water regulation, so called movement barriers, hamper the movement of aquatic organisms, especially fish (Baumgartner et al., 2009; Crook et al., 2009; Lassalle et al., 2009; Sutherland et al., 2013; Thompson et al., 2011). Fish are a crucial link in ecosystems as they influence substantial types of ecosystem services such as regulating food web

dynamics, nutrient and carbon fluxes, ecosystem resilience, sediment transport (Holmlund and Hammer, 1999). Not only are fish a crucial link in ecosystems, they are an economically important group of animals as well. Due to the growing human population, sufficient protein sources are crucial and the demand for fish is ever increasing (FAO, 2016). Consequently, fish are one of the most traded food items in the world and it is of utmost importance to manage their populations sustainably. This can be achieved by understanding their lifecycle and behaviour. To fulfil their lifecycle, many fish species move between different habitats, such as feeding habitat, spawning habitat and nurseries, encompassing extensive migrations in doing so. Regarding fish migration, distinctions can be made depending if species use solely freshwater environments, marine environments or move between the two:

- **Potamodromous:** fish spawn in the upper reaches of rivers and grow in the lower reaches (e.g. brown trout (*Salmo trutta fario* L.), European chub (*Squalius cephalus* L.))
- **Oceanodromous:** both spawning and growing phase occur in the marine environment (e.g. Bluefin tuna (*Thunnus thynnus* L.), Atlantic goliath grouper (*Epinephelus itajara* Lichtenstein)).
- **Diadromous:**
 - Catadromous: fish spawn in marine habitat and reach adulthood in freshwater habitats (e.g. European eel (*Anguilla anguilla* L.), Giant mottled eel (*Anguilla marmorata* Quoy & Gaimard))
 - Anadromous: fish spawn in freshwater habitat and reach adulthood in marine habitat (e.g. Atlantic salmon (*Salmo salar* L.), Atlantic sturgeon (*Acipenser sturio* L.))

- Amphidromous: fish spawn in freshwater habitat, larvae drift into marine habitats and migrate back into freshwater habitat to reach adulthood (Dolly Varden (*Salvelinus malma* Walbaum), mountain mullet (*Dajaus monticola* Bancroft)).

Being highly mobile animals, fish suffer when connectivity is constrained (Larinier, 2001; Drouineau et al., 2018a; Limburg and Waldman, 2009). Movement barriers can impact fish, and diadromous and potamodromous fish in particular, both on a transversal (i.e. influencing up- and downstream movement; e.g. by weirs, dams, pumping stations, shipping locks and sluices) as a lateral level (i.e. affecting fish movement from the river to flood plains and vice versa; e.g. by dykes) (Aarts et al., 2004; Drouineau et al., 2018a). Another aspect is mortality caused by hydropower plants, pumping stations and turbine stations (Buysse et al., 2014; Winter et al., 2006). Despite the development of fish-friendly pump adaptations and fish passages to reduce mortality (Buysse et al., 2015; Clay, 1994), the efficacy of many presumably fish-friendly adaptations remains to be established (Boggs et al., 2004; Gowans et al., 1999; Keefer et al., 2004; Marmulla, 2001; Roscoe and Hinch, 2010). Next to mortality effects, pumping stations may also affect migration behaviour, resulting in delays or even migration stops. Consequently, delays or migration stops may result in a higher predation risk or reduced fitness and therefore contribute to the decline of a species (Marmulla, 2001; Silva et al., 2018).

Polders are one particular ecosystem type where the role of barriers is crucial. A polder is an anthropogenic system where water is maintained at a lower level than outside the polder by pumping stations and weirs, which are two

types of barriers that can negatively influence migration of both diadromous and potamodromous fish species (Buysse et al., 2014; Falke and Gido, 2006). Due to climate change, the associated rising sea level and a growing human population, pressure on dewatering systems is likely to intensify in the future, resulting in the development of more polders with their accompanying movement barriers (Beatty et al., 2014; Hannah et al., 2007; Hermoso and Clavero, 2011; Maceda-Veiga, 2013).

Another widely distributed anthropogenic altered water body, are shipping canals for navigation and irrigation (Vitousek et al., 1997). Their number is likely to increase in the future due to climate change and a growing human population (Hannah et al., 2007). Canals are commonly characterised by a low structural variability (e.g. concrete embankments without riparian vegetation) with shipping locks, weirs and turbine stations, resulting in a regulated water flow. In addition to navigation, canals support industrial water management by facilitating water withdrawals and waste water disposal. It has already been shown that shipping canals may have a negative effect on local freshwater fish communities (Arlinghaus et al., 2002; Wolter and Arlinghaus, 2003). Such negative effects can be direct (e.g. shear stress, ship waves, dewatering and backwash...) or indirect (e.g. habitat fragmentation and simplification, loss of spawning and nursery habitats...) (see Wolter and Arlinghaus (2003) for an extensive review). Although the impact of shipping canals on non-migratory fish species has been extensively studied (Arlinghaus et al., 2002; Wolter, 2001; Wolter and Arlinghaus, 2003), knowledge on their effects on diadromous fish species remains poorly understood. Shipping canals generate threats for diadromous fish species: structures such as shipping locks, weirs and turbine stations, as well as the regulated water flow, may hamper migra-

tion behaviour (e.g. by disorientation). However, shipping canals may also provide alternative opportunities such as new migration routes, by connecting river basins or creating shorter migration routes to the sea. Depending on the impact of these canals on fish migration, proposed management measures could for instance include adjusted flow regulation or mitigation measures at turbine stations and shipping locks.

Providing numerous goods and services and playing a crucial role in fish life cycles, there is an urgent need to effectively restore aquatic ecosystems (Elliott and Whitfield, 2011; Postel and Richter, 2012).

1.3 Anguillid life cycle

A particular group of diadromous fish are the catadromous eels of the genus *Anguilla*, family Anguillidae, within the order Anguilliformes. They are of high interest for water management due to their role as flagship species. Specifically, since eels have a complex life cycle, they are sensitive to the five components of global change, i.e. climate change, habitat loss and fragmentation, pollution, introduced parasites and overexploitation (Drouineau et al., 2018b). As they can withstand a variety of environmental conditions, a density decline in a local catchment often indicates a substantial deterioration of the ecosystem functioning (Drouineau et al., 2018b). Consequently, when management takes actions to improve densities, other aquatic life will likely benefit from it as well (Feunteun, 2002; Simberloff, 1998). Also, since eels easily accumulate pollutants (Section 1.4.3), they are reliable bio-indicators for water pollution. They are, for instance, used to conclude on the chemical status of water basins

within the Water Framework Directive (Belpaire and Goemans, 2008; Belpaire et al., 2008).

Anguillid eels evolved between 70 million and 40 million years ago from a tropical deep sea ancestor (Aoyama et al., 2001; Inoue et al., 2010; Tsukamoto et al., 2002). Nowadays, the genus consists of 16 species of which three are further divided into two subspecies (Ege, 1939; Watanabe, 2003; Watanabe et al., 2004, 2005, 2009, 2014). They are found in both temperate, tropical and subtropical regions and all undertake excessive spawning migrations ranging between a couple of hundred to several thousands of kilometers (Arai, 2016). Despite the fact that spawning occurs in the ocean, Anguillid eels occur in both freshwater and marine systems, a trait likely evolved to exploit the relatively risk-free and productive freshwater habitats available in the tropics (Tsukamoto et al., 2002). Although being classified as catadromous, Tsukamoto and Nakai (1998) found that a part of the European and Japanese eel (*A. japonica* Temminck and Schlegel, 1846) do not swim up freshwater systems and therefore, both species can be considered facultative catadromous. The authors hypothesized that sea residency may be more common for temperate eel species due to the less productive fresh water systems, but further research is needed to confirm this hypothesis.

Spawning of anguillid eels is very similar among the different species and starts in a tropical sea. Since the European eel is the focus of this PhD dissertation, we will therefore explain the anguillid lifecycle of this species (Fig. 1.1). The distribution of the panmictic European eel population ranges from Northern Europe in Iceland and Norway over the Mediterranean to Northern Africa (Als et al., 2011; Dekker, 2003). Although nor spawning eels nor eggs have

been observed in the wild, it is assumed that the European eel spawns in the Sargasso Sea. The Sargasso Sea is located in the North Atlantic Ocean covering a relatively large area over one million square miles (ca 20–30°N, 48–79°W).

This assumption is made, since in the early 1900s a Danish scientist called Johannes Schmidt went on a campaign, fishing against the incoming waves of willow-shaped eel larvae, i.e. leptocephalus larvae (Fig. 1.2a) (Schmidt, 1922). It was in the Sargasso Sea that the smallest stadium (7 mm) of these larvae was found. The larvae drift with the eastward flow of the Gulf Stream, followed by the North Atlantic Drift towards the European continent and North Africa. It is near the continental slope that the leptocephalus larvae transform into glass eels, small eels lacking pigmentation (Fig. 1.2b) (Antunes and Tesch, 1997). Although it is unknown how long this trans-Atlantic migration takes, it is estimated to range between seven months and over two years, depending on the used method (Bonhommeau et al., 2010). Some glass eels will stay in coastal areas and estuaries (Tsukamoto and Nakai, 1998), while others will migrate upstream in rivers (Tesch, 2003). Due to their small size and accompanied weak swimming ability, it is unlikely they can migrate against the tides and river current for a very long time (Feunteun et al., 2008). Therefore, the glass eels make use of selective tidal stream transport (STST) to migrate upstream: they ascend into the water column during the appropriate tide and descend to the bottom during the reverse tide (Creutzberg, 1961; Trancart et al., 2012; Walker et al., 1978).

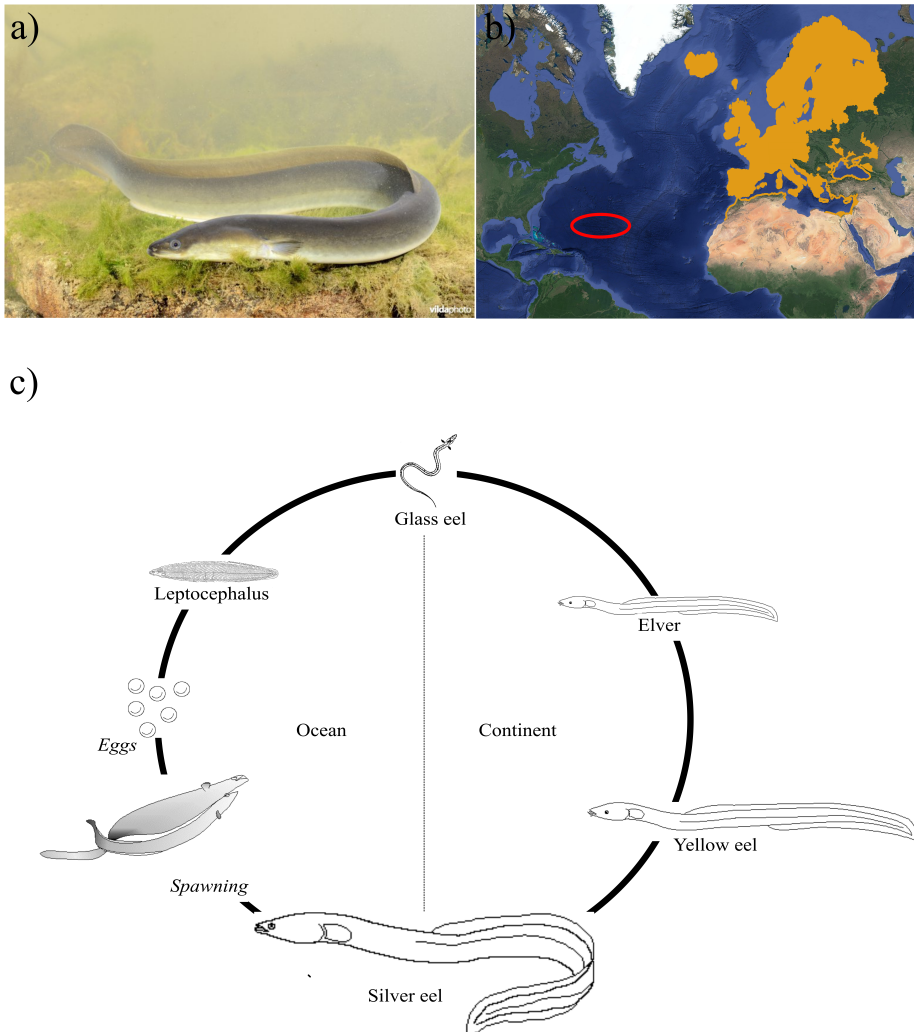


Figure 1.1: a) The European eel (photo credit: Rollin Verlinde) b) is distributed throughout Europe (orange-filled shape) and presumably spawns somewhere in the Sargasso Sea (red ellipse) (distribution data are obtained by IUCN and the spawning location is based on Miller et al. (2015)). c) The eel has a complex lifecycle with leptocephalus larvae drifting to continental Europe and North-Africa where they subsequently metamorphose in glass, yellow and silver eels to migrate back to the spawning location (source: Dekker (2008)).

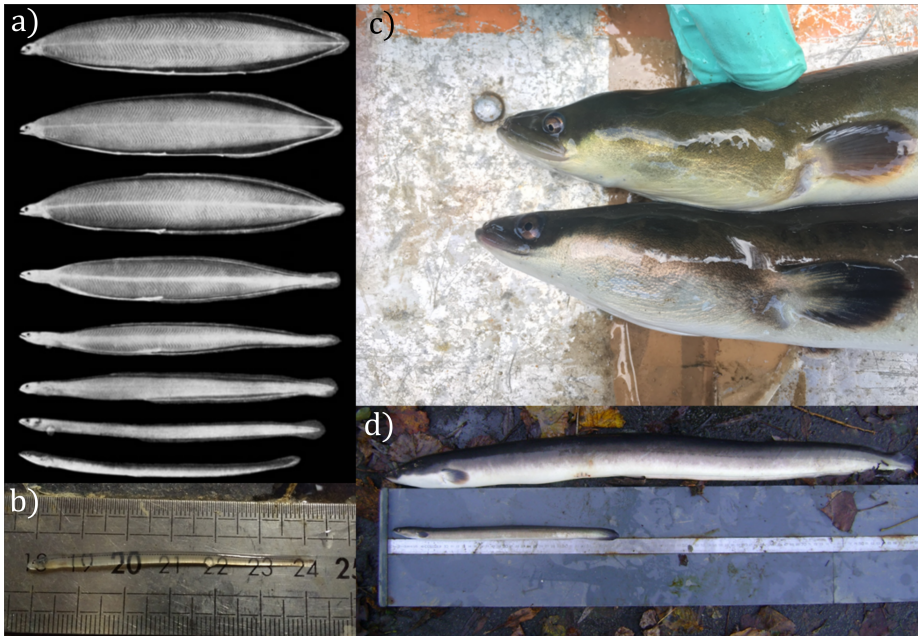


Figure 1.2: a) Gradual transition from a full grown leptocephalus larva to glass eels (figure adopted from Schmidt (1909)). b) A glass eel. c) The head region of a yellow (upper) and a silver eel (lower). Yellow eels have a yellowish colour, while silver eels are characterised by a grey back and white belly. Notice the enlarged eyes and pectoral fins of the silver eel. d) Eels show sexual dimorphism, with female silver eels (upper a 93 cm long female) growing much larger than males (lower a 38 cm male), which do not exceed 45 cm total length (Durif et al., 2005).

During the following stage, the glass eels start to pigment and develop into elvers, which in their turn grow as yellow eels (Fig. 1.2c). Yellow eels are rather sedentary with a limited home range and strong site fidelity (Baras

et al., 1998; McGovern and McCarthy, 1992; Walker et al., 2014). Yellow eels (but also the other life stages) are primarily nocturnal, hiding near the bottom in crevices and under branches during daytime, but diurnal movement during overcast weather has been reported (Baras et al., 1998; McGovern and McCarthy, 1992). During the growing stage, eel adopt an opportunistic feeding pattern, preying on insects and their larvae, molluscs, annelids, macroinvertebrates and fish (Lammens et al., 1985; Schulze et al., 2004; Sinha and Jones, 1967; Van Liefferinge et al., 2012). Based on what they eat, eels' head shape can differ, with narrow headed eels feeding on small/soft prey and broad headed eels on large/hard prey (De Meyer et al., 2016; Lammens and Visser, 1989; Pro-man and Reynolds, 2000). The morphological difference is attributed to the development of larger jaw closing muscles in broad headed eels (De Meyer et al., 2016). However, recent research indicated a genetic link with head shape as well (De Meyer et al., 2017b). Yellow eels grow for three to over 20 years in continental waters to accumulate fat before migrating back as silver eels to the spawning area (Boëtius and Boëtius, 1985; Tesch, 2003; Vøllestad, 1992). Silver eels are characterized by the silver white belly, dark grey back and enlarged eyes and pectoral fin (Durif et al., 2005). These morphological changes are an adaptation to the pelagic phase of this life stage. Notably, sexual dimorphism between male and female silver eels exists, with males not growing larger than 45 cm (Fig. 1.2d) (Dekker et al., 1998; Durif et al., 2005; Lobón-Cerviá et al., 1995). This can be explained by their different life strategy: females adopt a size-maximizing strategy by growing older and larger, while males adopt a time-minimizing strategy (Helfman et al., 1987; Vøllestad, 1992). The consensus is that silver eels migrate to the sea in autumn, although spring migration has been observed as well (Aarestrup et al., 2008; Sandlund et al.,

2017; Verbiest et al., 2012). Different environmental cues may trigger migration, such as water temperature, precipitation and discharge (Sandlund et al., 2017; Travade et al., 2010; Vøllestad et al., 1986). Migrating during a peak discharge enables the eels to save as much energy as possible for spawning itself, an important feature for a semelparous species. Especially since silver eels stop feeding during migration and even parts of their skeleton is resorbed to fulfill nutrient needs (Chow et al., 2010; Rolvien et al., 2016; Tesch, 2003). Once in the ocean, eels start to show a diel vertical migration pattern: at night they migrate higher in the water column and during daytime, they descend to deeper layers, a mechanism attributed to predator avoidance or thermoregulation (Aarestrup et al., 2009; Righton et al., 2016; Westerberg et al., 2007, 2014). Despite a lot of research on the European eel life cycle, many knowledge gaps still exist, preventing proper management. And notwithstanding the numerous tracking studies at sea (Amilhat et al., 2016; Righton et al., 2016; Aarestrup et al., 2009; Huisman et al., 2016; Westerberg et al., 2014), until now, a silver eel has never been tracked into its spawning site.

1.4 The European eel problem

Reports on the European eel decline of the continental stages (i.e. yellow and silver eels) date back to the early 1800s (Anonymous, 1865, 1867; Dekker and Beaulaton, 2015). The exact causes are speculative, but articles from the late 1800s and early 1900s indicate that habitat fragmentation and migration barriers may have played an important role (Adickes, 1888; Walter, 1910). For instance, Benecke (1884) already mentioned the construction of glass eel ladders

(see Section 1.5.3). It was, however, until the 1970s that a substantial decline in the glass eel recruitment was apparent, indicating a decline between 90% and 99% (Dekker and Casselman, 2014) (Fig. 1.3). This led to the species being listed as critically endangered in 2008 under the IUCN Red List (Jacoby and Gollock, 2014). Various causes likely contribute to this decline, among the most referred to in literature are movement barriers, habitat loss and deterioration, pollution, overexploitation, human-introduced parasites and changes in ocean climate (Clavero and Hermoso, 2015; Buysse et al., 2014; Feunteun, 2002; Køie, 1991; Miller and Tsukamoto, 2016; Moriarty and Dekker, 1997). It is hard to hierarchically order each cause of decline, especially since their impact can differ according to the geographical scale (habitats, countries and their water management...). Yet, a recent report indicates that fishing and non-fishing mortality may have a similar impact (ICES, 2016).

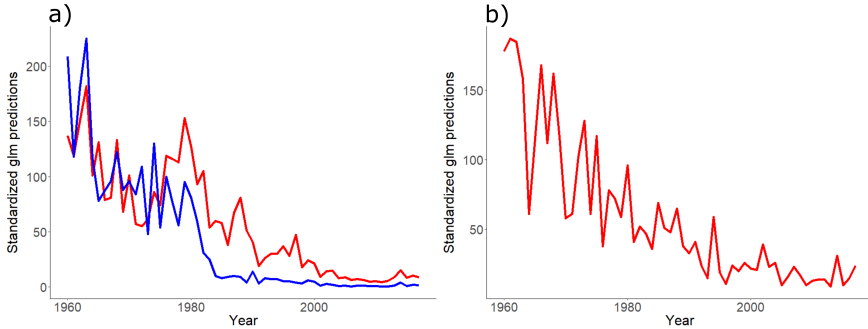


Figure 1.3: a) The recruitment decline of a) glass eels in the North Sea region (blue) and elsewhere in Europe (red), and of b) yellow eels in Europa. Recruitment values are geometric means from generalised linear model estimates. Data for the North Sea comprised data sets from Norway, Sweden, Germany, Denmark, The Netherlands and Belgium. Data from the UK, Ireland, France, Spain, Portugal, and Italy were used for elsewhere in Europe (ICES, 2018).

1.4.1 Movement barriers

Movement barriers pose an important threat to the European eel population on different levels such as inaccessibility of qualitative habitat, mortality, disorientation and delays (Feunteun, 2002; Moriarty and Dekker, 1997). The impact of each level varies with the eel's life stage, for instance, inaccessibility of qualitative habitat mainly poses a problem for glass eel colonisation and yellow eel ranging and migration behaviour, while barriers resulting in mortality, delays and disorientation mainly affect silver eel escapement.

Barriers hampering glass and silver eel migration are often referred to as

migration barriers. Moriarty and Dekker (1997) summarized that of the 123,798 km² potential eel habitat in Europe (both marine and freshwater, artificial and natural), 36,463 km² (29%) is inaccessible. More specifically, 82% of the eel habitat in the Iberian peninsula has become inaccessible since the 19th century, resulting in eels mainly occupying coastal zones (Clavero and Hermoso, 2015). It is, however, unknown what the population dynamics and eel movements were in the absence of movement barriers. For instance, land reclamation accompanied by the construction of dykes and pumping stations resulted in the loss of qualitative estuarine habitat such as salt marshes and lagoons. Further, construction of movement barriers prevents upstream migration of glass eels, elvers and yellow eels (Clavero and Hermoso, 2015). This may force upstream migrating eels to settle in coastal regions, leading to an adaptive mismatch between genotype and the occupied habitat. Specifically, it has been observed that glass eels, which were caught in coastal areas, but restocked in upstream locations, had a faster annual growth rate and migrated at a smaller size back to the sea compared to natural recruits (Stacey et al., 2015). Additionally, it is unknown if migration barriers influenced population dynamics in coastal areas, since both historical and current data on eel abundance and distribution in those areas is scarce and in many regions absent.

Migration barriers also affect silver eel escapement back into the sea. Many studies indicated a high mortality of silver eels passing through pumping stations or hydropower plants (Berg, 1986; Buysse et al., 2014, 2015; Larinier and Travade, 2002; Winter et al., 2006, 2007). Mortality rates vary among the mechanism used: propeller pumps, for example, can kill up to 97% of migrating silver eels, while this is near 20% for Archimedes pumps and hydropower turbines (Buysse et al., 2014, 2015; Winter et al., 2007). Next to direct mortality,

migration barriers and the accompanied regulated water flow may also lead to substantial delays (e.g. by disorientation), resulting in a higher predation risk or reduced fitness (Marmulla, 2001). However, the consequences of such delays on the eel's lifecycle are poorly understood and urgently require further research (Silva et al., 2018).

1.4.2 Habitat quality

It is beyond dispute that aquatic habitats have deteriorated since the Industrial Revolution. Not only limit connectivity constraints suitable habitat for eels (Larinier, 2001), deterioration is mainly caused by, for instance, land reclamation, canalization and dredging (Aarts et al., 2004; Feunteun, 2002). Canalization in particular results in a low structural variability (e.g. concrete embankments without riparian vegetation). The function of canals is diverse and includes amongst others navigation, support of industrial water management by facilitating water withdrawals and waste water disposal. It has already been shown that shipping canals may have a negative effect on local freshwater fish communities (Arlinghaus et al., 2002; Wolter and Arlinghaus, 2003). Such negative effects can be direct (e.g. shear stress, ship waves, dewatering and backwash...) or indirect (e.g. habitat fragmentation and simplification, loss of spawning and nursery habitats...) (see Wolter and Arlinghaus (2003) for an extensive review). Nonetheless, qualitative habitat characterized by a network of rivers, connected ponds and ditches, results in a high habitat diversity and thus many potential growth areas for yellow eels (Lasne et al., 2008). This could lead to higher growth rates, and larger eels have a higher survival rate (Boulenger et al., 2016). Even more, areas located close to the sea may, in the

absence of migration barriers, be easily colonised by glass eels (Laffaille et al., 2004). Yet, little is known about the importance of qualitative habitat for eels, especially for the sedentary yellow eel stage (Laffaille et al., 2005).

1.4.3 Pollution

Related to habitat deterioration, are the high abundance and diversity of pollutants flushed yearly into marine and aquatic systems, where they especially bind to sediment particles (Cooper, 1993; Schwarzenbach et al., 2006; Weis, 2014). Being a benthic species and due to their high fat content, eels are prone to bioaccumulation of lipophilic pollutants (Belpaire, 2008; Belpaire et al., 2008). It is unlikely that eels die from pollutant bioaccumulation (except from spills or accidents, (Bálint et al., 1997; Christou, 2000; Knights, 1997)), yet, pollution can have sublethal effects. A lot of research has been conducted in this field and effects on various physiological systems have been indicated, a.o. immune, nervous, endocrine and reproduction system (see Geeraerts and Belpaire (2010) for an extensive review). Pollution may constrain successful spawning migration since they stop feeding during spawning migration and therefore rely on their fat reserve (Belpaire et al., 2016; Chow et al., 2010). Consequently, it has been suggested that as lipid deposits are depleted during migration, lipophilic contaminants are released into the blood and interfere with the eel's physiology, impacting vital organs and gonads among others (Larsson et al., 1991). Luckily, due to waste water treatment, water quality is improving (Thyssen, 2001), which has been reflected by the decrease in pollutant concentrations in eels (de Boer et al., 2010; Maes et al., 2008). Yet, it is unknown if current concentrations affect eel reproduction (Knights, 1997), especially since

new pollutants are emerging.

1.4.4 Overexploitation

Eels are an important product for human consumption and their exploitation dates far back to 1086 (Dekker, 2018; Dekker and Beaulaton, 2015). It was not until the late 1800s that eel fisheries expanded substantially by modernisation and commercialisation, leading to larger catches with a peak of over 20,000 tonnes annually exploited eels in Europe during the 1960s (Dekker, 2018). Yet the yields have dropped substantially since the recruitment decline in the 1970s, being nowadays around 8,000 tonnes (Fig. 1.4) (FAO; <http://www.fao.org/fishery/species/2203/en>). Every continental phase of the European eel (i.e. glass, yellow and silver eels) is exploited and is often region specific. Glass eels, for instance, are fished in countries near the Bay of Biscay where their abundance still reaches the highest numbers, while yellow and silver eels are fished throughout the eel's distribution range (Dekker, 2016).

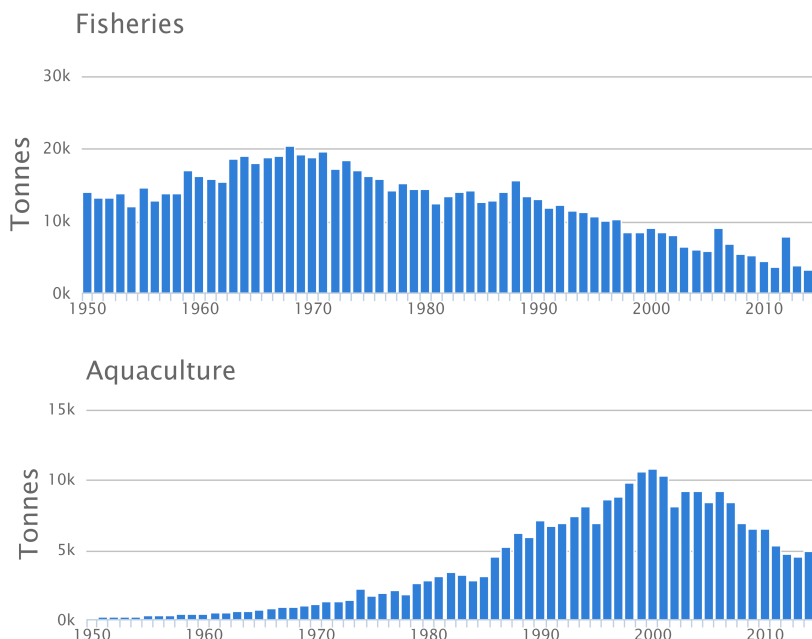


Figure 1.4: Global fisheries and aquaculture production of the European eel (figure adopted from <http://www.fao.org/fishery/species/2203/en>).

Glass eels are caught for both direct consumption (a delicacy called 'anguilas' in Spain; in 2016s fishing season, the first 1.25 kg caught glass eels were sold for €5,500) and as seedlings for aquaculture facilities; the latter producing nowadays up to 5,000 tonnes of eels per year and therefore comprise the largest part of eel exploitation. Since it is not yet possible to breed European eels in captivity, the aquaculture sector still depends on the recruitment of the wild population for production, limiting its productivity. Due to the high Asian eel demand and the related decline of the Japanese eel stock, a lot of illegal traffick-

ing exists of European glass eels to Asia. It is estimated that 10 tonnes of glass eels have been smuggled from Europe to Asia during the 2016-2017 fishing season (Anonymous, 2017a). Further, yellow and silver eels are both commercially caught with various fishing techniques (e.g. fyke nets, eel pots, stow nets...) to create eel products like jellied, smoked and fried eels (the latter with a green sauce based on seven green herbs is considered a delicacy in Flanders). Next to commercial fishing, in some European countries recreational fishing for eels exist by means of line fishing or bobbing. Although total yields from recreational eel fisheries are hard to quantify, an extraction of 30 tonnes per year was estimated based on a questionnaire in Flanders (Belgium) in 2016 (ICES, 2017). This in spite of a negative governmental advice due to high pollutant levels in eels. Obviously, exploitation has an impact on the eel population. Some studies have indicated that silver eel fisheries substantially impede the number of escaping silver eels (Aarestrup et al., 2010; Moriarty and Dekker, 1997).

1.4.5 Parasites

A possible biological contributor to the European eel decline, is the introduction of the Asian parasitic swim bladder nematode *Anguillicoloides crassus* (Kuwahara, Niimi and Itagaki, 1974) Moravec and Taraschewski, 1988. This species was introduced in Europe during the eighties likely with import of its native host, the Japanese eel, for consumption and restocking by foreign infected European eels (Belpaire et al., 1989). Once the eels consumed infected cyclopoid copepods, the intermediate host, *A. crassus* larvae move from the intestines into the swim bladder, where they feed on blood, grow till adulthood

and reproduce (De Charleroy et al., 1990). *A. crassus* infection involves tissue scarring, leading to a lower swim bladder elasticity and an accompanied enlarged chance of rupture. Since eels apply extensive diel vertical migrations in the ocean spanning a vertical depth range over 500 m, infection may impair spawning migration (Aarestrup et al., 2009; Barry et al., 2014; Righton et al., 2016). Indeed, experiments by Palstra et al. (2007) suggested that infected eels show lower swim speeds and higher migration costs. Yet, a recent telemetry study in the North and Baltic Sea compared migration behaviour between an infected eel with three non-infected eels and indicated a minor impact on migration behaviour by the parasitic nematode (Simon et al., 2018).

1.4.6 Climate change

Human activities have a substantial impact on climate change, affecting marine ecosystems and influencing marine currents (Böning et al., 2008; Halpern et al., 2008). Ocean climate change likely plays an important role in the glass eel recruitment decline as well (Arribas et al., 2012; Bonhommeau et al., 2008; Feunteun, 2002; Knights, 2003; Miller and Tsukamoto, 2016). Warm winters, for instance, lead to a lower productivity in the Sargasso Sea (Bates, 2001), which may lead to starvation of leptocephalus larvae (Bonhommeau et al., 2008). Also, changes in currents, resulting in a prolonged migration phase, might make leptocephalus larvae more prone to diseases and predation, exacerbating eel recruitment (Kettle et al., 2008; Knights, 2003; Moriarty and Dekker, 1997). Notably, due to their opportunistic behaviour, eels are likely less influenced by continental climate change (Knights, 2003; Schulze et al., 2004; Van Liefferinge et al., 2012). Even more, Knights (1997) speculated that an in-

crease in continental temperature may favour eel growth. He also speculated that a precipitation increase in Northern Europe may favour silver eels runs, yet, a dryer climate in the south may have the opposite effect.

1.5 The European Eel Regulation and current management

To aid conservation and recovery of the European eel population, the European Union adopted a Council Regulation (European Eel Regulation; EC no. 1100/2007) which imposes a management system that ensures 40% escapement of the spawning stock biomass, defined as the best estimate of the theoretical escapement rate if the stock were completely free of anthropogenic influences. To do so, the Regulation proposes actions at several levels of the nationally defined "eel river basins" (i.e. each EU Member State identifies natural habitat for the European eel within their national territories), resulting in national Eel Management Plans (EMPs): reducing commercial and recreational fisheries, restocking measures, improving aquatic connectivity and habitat quality, translocating silver eels to areas from where they can freely migrate into the marine environment, combatting predators, temporary switching off hydropower stations and aquaculture measures. Consequently, 20 countries developed EMPs (Belgium, Denmark, Estonia, Finland, France, Germany, Greece, Ireland, Italy, Latvia, Lithuania, The Netherlands, Norway, Poland, Portugal, Spain, Sweden, Tunisia, Turkey and the UK), which are under the international supervision of the ICES Eel Working Group (WGEEL).

1.5.1 Exploitation limitations

As mentioned above, eel fisheries target all life stages and exploitation pressure varies among geographical regions (Table 1.1). Considering glass eels and elvers, the EU Eel Regulation demands that 60% of the annual caught eels < 12 cm are traded for stocking purposes only. In addition, due to a continuing decline in eel recruitment, glass eel export outside of Europe became prohibited from 2010 onwards; especially Asia was an important consumer. Yet, the illegal trade of European glass eels to Asia hinders efficient management. Actions to reduce fishing mortality of yellow and silver eels include national eel quota, adapted fishing gear, restricted fishing periods and areas, and a minimum size; which all differ according to national measurements. Since it would be too exhaustive to delineate the fisheries policy of all 20 countries, we refer to the WGEEL report of 2017 for an extensive overview (Anonymous, 2017d). Nonetheless, we summarise the policies of four countries (Belgium, Ireland, The Netherlands and UK) to illustrate its diverseness.

- In Belgium, there is no commercial fishing for eels anymore and in Wallonia, the southern part of Belgium, recreational fishing for eels is prohibited. In Flanders it is allowed by hand line fishing and bobbing; fyke and eel pot fishing is prohibited and therefore considered as poaching. A fisherman is allowed to take maximum five eels of minimum 30 cm per fishing session.
- In Ireland, commercial eel fisheries were closed after the EU Eel Regulation implementation. Some recreational fishery exists, but its impact is considered low, especially since there is no eel culture in Ireland.

- In The Netherlands commercial fishing is allowed in specific areas (i.e. areas free from or with tolerable levels of pollution). Yet, it is prohibited from September till December to maximise silver eel escapement. The minimum landing size of an eels is 28 cm. Recreational eel fishing is prohibited in inland waters and when caught, eels have to be retrieved immediately into the water they were caught from.
- Apart from the glass eel fisheries in the UK, commercial yellow and silver eel fisheries exist by licensed fishermen, handling a minimum size of 30 cm and fishing from 1st April till the 15th of February. Recreational eel fishing is allowed, however, all eels have to be released alive in the water they came from.

Next to these national measurements, the Council of Europe recently agreed to close fisheries on European eel > 12 cm in Union Waters of ICES areas for three consecutive months between 1 September 2018 and January 2019; the onset of those three months can be determined by each country independently (Anonymous, 2017b).

Being an exploited species, the Sustainable Eel Group (SEG) is working on a sustainable eel label, based on the MSC label: the SEG Standard (<http://www.sustainableeelgroup.org/seg-standard/>). The goal of the label is, as stated from their website, “To maximise the contribution of eel fishers, ranchers, aquaculturalists, traders and consumers of eel products to the restoration of healthy eel populations, distributed throughout their natural range, fulfilling their role in the aquatic environment and supporting sustainable use for the benefit of communities, local economies and traditions”. Further, the Eel

Stewardship Fund (ESF) helps funding eel management practices (e.g. buying glass eels for restocking) or eel research with the profits from the trade of ESF labelled eels (e.g. €1 from the selling price of ESF labelled eels in the supermarket is used for eel conservation or research).

Table 1.1: Overview of the commercial and recreational fishing allowances for the 20 countries in the EU Eel Regulation after Anonymous (2015) and Anonymous (2017d). Note however, that some countries do not make a distinction between yellow and silver eel fisheries. Also, recreational eel fishing data is not always available. Therefore, it is considered permitted for consumption unless stated otherwise.

Country	Commercial fishing			Recreational fishing	
	Glass eel	Yellow eel	Silver eel	Catch & Release	Consumption
Belgium					x
Denmark		x	x		x
Estonia		x	x		x
Finland					x
France	x	x	x		x
Germany		x	x		x
Greece			x		
Ireland					x
Italy	x	x	x		x
Latvia		x	x		x
Lithuania		x	x		x
The Netherlands		x	x		
Norway		x			
Poland		x	x		x
Portugal	x	x			x
Spain	x	x	x		x
Sweden			x		x
Tunesia		x	x		x
Turkey		x	x		x
UK		x	x	x	

1.5.2 Restocking and redistribution

As already mentioned above, 60% of the commercially caught glass eels are destined for restocking purposes. In the 1980s, glass eel restocking reached a peak, followed by a decline until 2010 when the EU Eel Regulation was implemented (Anonymous, 2017c) (Fig. 1.5). The recent increase was due to lower market prices, leading to higher numbers within the fixed stocking budgets. In Belgium for instance, from 2008 till 2017, 117 - 540 kg glass eels have been stocked annually, equalling €59,670 – 83,945 (Anonymous, 2017d).

Despite the substantial restocking effort, its impact on European eel recovery is dubious. Dekker and Beaulaton (2016) extensively summarized and reviewed 175 years of glass eel restocking in Europe and concluded that the measure only moderately contributed to the fishing yield, partly compensated the recruitment decline and did not improve spatio-temporal distribution substantially. Although post-evaluation of glass eel restocking is scarce, Ovidio et al. (2015) observed that glass eels in Belgian tributaries had grown and dispersed substantially one year after restocking. In that respect at least a part of the restocked glass eels can manifest themselves. Nonetheless, only a fraction of elvers ($n = 130$) was caught the year after restocking (2.5 kg glass eels were stocked, with an estimated $n = \pm 10,387$), which may be attributed to natural mortality by predation and disease, ranging outside the range of the study area and inefficiency of electrofishing for catching glass eels (Ovidio et al., 2015). Yet, failed short-term adaptation of glass eels into their new environment is not excluded. Although glass eel and elver survival rate was 100% after translocation from estuarine conditions in the wild to fresh, 50% and 100% salt water in an experimental design (Crean et al., 2005), Stacey et al. (2015) found

that stocked American glass eels had a faster growth rate, led to a different sex ratio and matured at smaller sizes and earlier ages than their naturally recruited conspecifics. They hypothesized that, despite being a panmictic species, life-history traits are attributed to selection during ingress migration, i.e. the spatially varying selection hypothesis. Therefore, spawning contribution of stocked eels may be limited and questions stocking as an efficient management measure over large geographical areas. Stacey et al. (2015) suggests to apply restocking within the same catchment to overcome migration barriers.

Further, the orientation mechanisms of migrating silver eels are not fully understood and the hypothesis of an imprinted map during glass eel migration still exists. Translocating glass eels to areas thousands of kilometers from their capture location may therefore result in disorientation during migration and unsuccessful spawning. Westin (1990), for instance, found that silver eels developed from stocked glass eels missed the outlet of the Baltic during a tracking study. In contrast, Westerberg et al. (2014) observed no significant difference in migration behaviour between silver eels from stocked and naturally recruited glass eels.

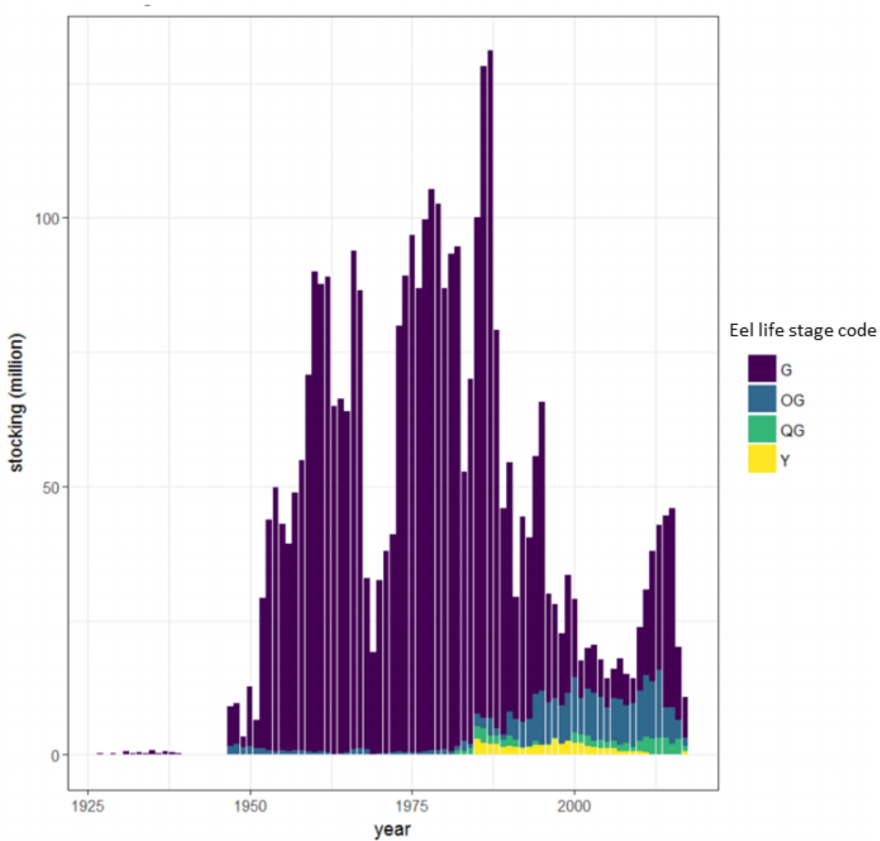


Figure 1.5: The number of eels stocked from 1925 till 2016 (G: glass eels; OG: ongrown eels; QG: quarantined eels; Y: wild caught yellow eels) (figure adopted from Anonymous (2017c)).

Another reason why glass eel restocking is not effective, is due to the various factors affecting eel survival (Section 1.4). Moving glass eels from coastal areas to tributaries overcome migration barriers during upstream migration of glass eels and elvers, but does not solve the problem for downstream migra-

tion in the silver eel stage. However, note that catching silver eels upstream of a migration barrier to transport them to a part of the river free of migration barriers is an applied management measure (i.e. "trap-and-truck") (McCarthy et al., 2008; Richkus and Dixon, 2002). Yet, this is very labour intensive and requires therefore substantial human interference, including stress during the catching and transportation process. Nonetheless, as long as there is no adequate solution implemented for all possible stressors, it will be hard for the eel population to recover (Drouineau et al., 2018b).

1.5.3 Improving connectivity

The eel's lifecycle encompasses two migration phases in freshwater: upstream migration as glass eels, elvers and yellow eels to colonize suitable growing habitats and downstream migration as silver eels to reach the sea for spawning (Nzau Matondo and Ovidio, 2016; Tesch, 2003). Consequently, solving migration barriers need to act on both phases.

The majority of the fish passes constructed for upstream migrating fish, target strong and fast swimmers such as anadromous salmonids and shads (Beach, 1984; Larinier and Marmulla, 2004). Several types exist, often accompanied with a strong current acting as a guiding cue: pool type, Denil or baffle type, De Wit and nature like fish passes (Larinier and Marmulla, 2004; Viaene et al., 2004). Due to their small size and accompanied weak swimming ability, it is unlikely that glass eels can migrate against the strong currents present in fish passes for a very long time (Feunteun et al., 2008). A popular construction to aid upstream glass eel migration, are eel ladders (Legault et al., 1990; Benecke, 1884). The construction consists of a slope, often under 15° - 45°, with specific

substrate (e.g. nylon bristles or coconut mats) overrun by water (Legault, 1992; Solomon and Beach, 2003). The concept is that glass eels detect the flow, migrate/crawl up the slope and consequently overcome a migration barrier such as a dam, weir, pumping station or tidal sluice. Such a management measure often requires human interference by translocating the collected glass eels in a reservoir at the end of the ladder over the migration barrier. In addition, crawling up a slope may increase predation, disease or stress, resulting in a higher mortality. Another management action recently applied, is adjusted tidal barrier management (Mouton et al., 2011b). During the glass eel migration season, tidal barriers are opened ajar (e.g. 10 cm) during high tide to allow glass eel intrusion. The study of Mouton et al. (2011b) observed no conductivity increase upstream during implementation of the management measure.

Once reaching maturity, silver eels commence their downstream migration, encountering numerous migration barriers. As mentioned above (Section 1.4.1), pumping stations and hydropower turbines cause substantial mortalities and injuries in downstream migrating fish. Consequently, management measures are being developed. In a specific Belgian polder area, an Archimedes pumping station got fish-friendly 'de Wit' adaptations by applying curved edges on the first windings of the screws, which should lead to less blade strikes (Buysse et al., 2015). Yet, no significant difference in eel mortality was found before the measurement was taken (Buysse et al., 2014). Due to the high mortality caused by turbines, some hydropower plants are shut down during the silver eel migration season, sometimes accompanied by a MIGROMAT (i.e. silver eels held in a container to monitor their activity) (Adam, 2000). However, due to the accompanied substantial economic losses, this is not always feasible. Further, management measures are taken to prevent eels from

migrating through pumps and turbines, for example by eel racks (Russon et al., 2010) and light deflection systems (Hadderingh et al., 1999, 1992). Nonetheless, when deflected, eels still need to overcome the barrier. Fish bypasses for upstream migration rarely work in the opposite direction, likely because downstream migrating fish follow the main flow instead of seeking for a specific cue, like the repellent current downstream from a fish pass. Consequently, research and development of efficient downstream fish passes is urgently needed (Feunteun, 2002; Larinier and Marmulla, 2004; Solomon and Beach, 2003). One applied practice to overcome migration barriers is catching silver eels and transporting them to an area from where they can freely migrate into the sea (i.e. trap and transport) (Moriarty and Dekker, 1997). Yet, this method is very labour intensive and may induce stress, negatively influencing the eel's fitness. A non-labour intensive approach was recently found by Egg et al. (2017), who pointed out that eels can safely pass hydropower plants via an undershot weir. Nonetheless, technical constraints may inhibit the construction of undershot weirs, consequently there is an urgent need for more and other effective cost-efficient solutions.

1.6 Research objectives and outline of the PhD thesis

Despite the establishment of the EU Eel Regulation in 2007, the European eel population reached a historical minimum and many knowledge gaps remain (Dekker, 2016). With the improving water quality resulting from the Water Framework Directive and eel management mainly focusing on overexploita-

tion and restocking, an important bottleneck in eel management is movement behaviour related to suitable habitat (i.e. yellow eel movement behaviour) and migration barriers (i.e. silver eel migration behaviour). Adequate mitigation measures to improve the silver eel escapement rate require proper insight in both (1) yellow eel movement behaviour in nursery areas and (2) silver eel migration behaviour and how these are affected by current management practices.

The objective of this thesis is to investigate movement behaviour of large female eels, both in their yellow (i.e. sedentary) and silver (i.e. migratory) stage. Namely, to investigate movement behaviour, eels were tagged with acoustic transmitters. Due to the transmitter size and our restriction not to allow tags to exceed 2 % of the fish weight, the tagged eels were all large and considered to be females (minimum TL of 495 mm and minimum weight of 246 g) (Laffaille et al., 2003), as males are smaller than the minimum size handled in this study (<450 mm (Durif et al., 2005)). Movement behaviour of yellow eels may provide insight in the amount of space yellow eels require to grow. Consequently, the results can inform managers about sufficient qualitative and quantitative growing habitat. Once metamorphosing in silver eels, knowledge about their spatio-temporal migration behaviour is crucial for effective management trying to achieve a higher escapement-rate. The latter may consist of temporal elevation of migration barriers to the development of downstream fish passes. Consequently, the following general research questions are the focus of this dissertation, with more specific questions under the different chapters and subchapters:

- What is the spatio-temporal movement behaviour of the European

eel during the sedentary, yellow eel stage?

- What is the spatio-temporal movement behaviour of migrating eels in:
 - a system free of anthropogenic migration barriers?
 - moderately (e.g. polders) and severely (e.g. shipping canals) regulated systems?

Chapter 2 - Acoustic telemetry

Acoustic telemetry was the technique used to study spatio-temporal movement behaviour of European eels in this dissertation. In chapter two we explain the concept, applicability and some constraints of the technique.

Chapter 3 - Movement behaviour of large female yellow European eel (*Anguilla anguilla* L.) in a freshwater polder area

In this chapter, we analysed the movement behaviour of female yellow eels in a freshwater polder system, characterized by interconnected canals, polder ditches and ponds. A high density network of acoustic listening stations (ALSs) allowed to investigate (i) when yellow eels were most active in terms of circadian inter-ALS movements and seasonal swim distance patterns, including effects of temperature, (ii) the size of the movement range and (iii) what environmental variables determined movement. In addition, (iv) an effect of habitat type (i.e., canal, polder ditch and pond) on (ii) and (iii) was analysed.

Chapter 4 - Unimodal head-width distribution of the European eel (*Anguilla anguilla* L.) from the Zeeschelde does not support disruptive selection

The following chapter handles head width distribution of eels in the Schelde Estuary. Being opportunistic feeders, we hypothesize that eels from a single river drainage do not show disruptive selection related to eel head width by

assessing four sub-hypotheses: (i) Head width variation follows a unimodal distribution and (ii) this distribution does not differ between different maturation stages; (iii) body condition does not differ according to head width, and (iv) eels with a narrower head width migrate at a similar speed as eels with a broader head width.

Chapter 5 - Selective tidal stream transport in silver European eel (*Anguilla anguilla* L.) – Migration behaviour in a dynamic estuary

The fifth chapter related to spatio-temporal migration behaviour deals with movement in a system free of physical anthropogenic barriers, i.e. the Schelde Estuary, and can consequently be regarded as the baseline. Specifically, we investigated (i) if migratory eels apply STST and (ii) at what speed they migrate through the estuary.

Chapter 6 - Downstream migration of European eel (*Anguilla anguilla* L.) in an anthropogenically regulated freshwater system: Implications for management

In this chapter, we analysed the migration behaviour of female silver eels in a moderately regulated system, i.e. a polder. We analysed (i) if eels take different migration routes, (ii) if their behaviour changes significantly in the vicinity of barriers, (iii) if migration follows a circadian pattern, (iv) if migration starts at a specific point in time, and (v) what environmental variables influence migration.

Chapter 7 - European silver eel (*Anguilla anguilla* L.) migration behaviour in a highly regulated shipping canal

Chapter 7 deals with eel migration in a highly regulated shipping canal i.e. the Albert Canal, characterised by seven shipping lock complexes, turbine stations

and tidal sluices. In this chapter, we analysed if (i) eels are able to migrate out of the system, (ii) if they are delayed in their migration, and (iii) how their behaviour related to eel migration behaviour in other systems.

Chapter 8 - Heading south or north: novel insights on European silver eel *Anguilla anguilla* migration in the North Sea

The majority of eel telemetry research is conducted in freshwater and estuarine habitats. Consequently, the exact migration routes and destination of European eels are still unknown. In chapter 8, we describe a newly discovered marine migration route based on eels tagged in three different European countries (i.e. Belgium, Germany and The Netherlands).

Chapter 9 - General discussion

In the general discussion, first some nuances are made related to the applied methodology in this dissertation such as eel life stage classification and migration identification. Next, we discuss what the results can mean for future management, research and development. Finally, remaining knowledge gaps important for future research and management are discussed.

Chapter 10 - Conclusion

The conclusion states more of a plea why European eel management is failing and what needs to happen to be successful.

Chapter 2

Telemetry

2.1 Animal biotelemetry

Telemetry is an increasingly applied technique to investigate the behavioural ecology of aquatic animals in the wild and has benefited substantially from miniaturization and software development (Hussey et al., 2015). The word 'telemetry' is derived from the Greek *tele*, which means (from a) distance, and *metron*, meaning measurement. As such, telemetry involves collection of data on organisms from a distance.

Telemetry allows researchers to analyse animal behaviour at the individual level. By linking environmental and/or physiological data to the obtained telemetry data, researchers can get a better understanding of ecosystem functioning (Hussey et al., 2015; Lennox et al., 2017). This can help to assess the effects of anthropogenic disturbance by, for instance, man-made constructions (Piper

et al., 2017; Reubens et al., 2014; Winter et al., 2007) and thus can deliver the necessary insights for efficiently managing, restoring and conserving aquatic species and habitats (Hussey et al., 2015; Lennox et al., 2017). The resulting data and knowledge form the scientific basis for international policies and directives, such as the Common Fisheries Policy and the Integrated Maritime Policy, Natura 2000, Marine Strategy Framework Directive and the Water Framework Directive, among others (Hussey et al., 2015; Lennox et al., 2017).

Multiple biotelemetry techniques are available to track aquatic animals, each with its specific applications and limitations. Passive integrated transponder (PIT) telemetry, for instance, does not use an internal battery, since the emission signal is generated via an external antenna through which the transmitter needs to pass (i.e. a loop). The main advantage is the production of very small transmitters (< 1 cm in length), but the disadvantage is that antennas need to be built. This is feasible in small river stretches and to some extent in larger rivers (e.g. the NEDAP Trail System® which is a derivation of PIT telemetry), but it is impossible to apply this method in large estuaries and at sea. Other techniques require internal batteries in the transmitter, substantially increasing the transmitters' size. Transmitters applied in radio telemetry transmit radio waves and can be detected by antennas. However, radio waves rapidly attenuate in salt water, restricting the method to freshwater systems. Transmitters of acoustic telemetry on the other hand, emit acoustic signals which can be transferred to ALSs in salt water as well. This may partly explain why it is one of the most popular techniques to track aquatic animals and generate detailed spatio-temporal observations of their movements (e.g. dispersion, migration and homing) and habitat use (Hussey et al., 2015). Obviously, this telemetry technique is appropriate to track diadromous species

which move between freshwater and marine environments.

Next to transmitters, some techniques use data storage tags which store environmental data via sensors. Based on these data (mostly water temperature, light and pressure/depth), the tagged animal's trajectory can be estimated (Bonfil et al., 2005; Righton et al., 2016). To retrieve data from data storage tags, the tag needs to be retrieved. However, satellite archival tags have the ability to transmit the collected data to the ARGOS satellite (<http://www.argos-system.org>), which in turn transmits the data to the processor of the researcher. Since not all aquatic animals surface, pop-up functionalities have been developed for both conventional data storage tags and satellite archival tags. This facilitates that tags wash ashore and can be found by beachcombers and -goers (especially for data storage tags) or that the data are transmitted to the ARGOS satellite when non-surfacing animals are studied. This technique allows long-distance tracking of animals where the mooring of listening devices (e.g. acoustic telemetry, see 1.2) is impossible. However, the pitfall of the technique is that in order to estimate the trajectory of a tagged fish, based on measured environmental variables, high-resolution spatio-temporal data of the environment is a prerequisite. This is rarely the case in freshwater systems. For example, in a polder area in Flanders (see chapter 5), environmental data is measured at most two locations. Also environmental data in the Belgian Albert Canal lacks resolution (i.e. not all environmental variables are measured at all canal sections) or quality (see Chapter 6). Finally, there are electronic tags that combine features of different tags, such as radio-acoustic transmitters (Niezgoda et al., 1998) or the recently developed data storage tags with acoustic emissions.

Since eels move between freshwater and marine environments, and we were interested in environments which are often not monitored at a high spatio-temporal resolution, we decided to apply acoustic telemetry to answer our research questions.

2.2 Applicability of acoustic telemetry in aquatic systems

Acoustic telemetry uses ALSs which detect tagged animals autonomously by registering the transmitter ID, date and time (and sensor data when applicable) (Fig. 2.1). Consequently, this passive technique results in an Eulerian data approach (i.e. fixed stations detect a moving object (Merki and Laube, 2012)), unless active tracking or a dense, fine scale positioning system is applied (Roy et al., 2014). Transmitters come in variable sizes (both length and diameter), ranging from one to several centimeters, dependent on the acquired battery life time, which is related to the research question (e.g. long term vs short term tracking). Battery life time is also dependent on the transmitter settings, such as the minimum and maximum signal emission rate, sensors (e.g. pressure, temperature, accelerometer and predation sensor) and energy output (low or high). Transmitters are preferably surgically implanted in the abdominal cavity to avoid transmitter loss, lesions or biofouling leading to infections, yet this is not always possible dependent on the species (see Chapter 10 for an example of external tagging).

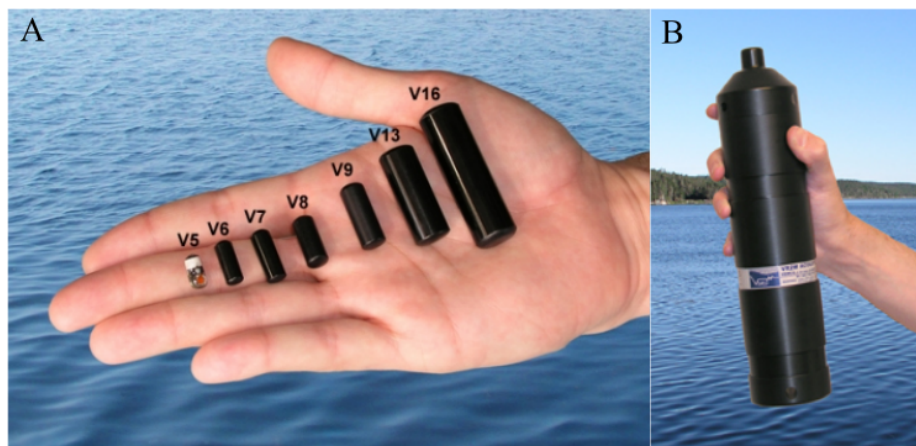


Figure 2.1: Different models of acoustic tags (A) and an acoustic listening station, model VR2W (B) from VEMCO Ltd (Canada) (Photo credit: VEMCO Ltd).

To tag the eels, we followed the protocol by Thorstad et al. (2013): first, fish are placed in a basin with an anaesthetic (e.g. clove oil, MS222 or phenoxy-ethanol; in this PhD dissertation, 0.3 ml L^{-1} clove oil was applied). When sedated, an incision is made to reach the abdominal cavity (Fig. 2.2). After implanting the transmitter, three stitches with non-absorbable monofilament close the wound. Subsequently, the wound is disinfected with isobetadine and the fish is placed in a reservoir for recovery, which takes approximately 30 min. Although we strived for a transmitter weight : body weight ratio of 2%, higher ratios do not lead to significant differences in swim speed (Brown et al., 1999). Yet, this led to the fact that we only tagged relatively large, female eels, as males are smaller than the minimum size handled in this study ($<450 \text{ mm}$ (Durif et al., 2005)). Further, transmitter expulsion is possible via the incision, an intact body part or the digestive system (Jepsen et al., 2002), but occurred in

only 12% of the eels in a study by Thorstad et al. (2013).



Figure 2.2: Acoustic transmitters are surgically implanted in the abdominal cavity (A) and the wound is subsequently closed with three non-absorbable monofilament threads (B). Eels recaptured after ± 1 year indicated they healed well from the surgery (C).

2.3 The need for aquatic telemetry networks – The Belgian case

Submitted as:

Reubens, J.; Verhelst, P.; van der Knaap, I.; Wydooghe, B.; Milotic, T.; Deneudt, K.; Hernandez, F.; Pauwels, I. The need for aquatic telemetry networks – The Belgian case. *Animal Biotelemetry*, under review.

P. Verhelst contributed to writing and generation of the figures.

2.3.1 Abstract

Aquatic biotelemetry techniques have proven to be valuable tools to generate knowledge on species behaviour, gather oceanographic data and help in assessing effects from anthropogenic disturbances. These data types support international policies and directives, needed for species and habitat conservation. As aquatic systems are highly interconnected and cross administrative borders, optimal data gathering should be organized on a large scale. This need, triggered the development of regional, national and international aquatic animal tracking network initiatives around the globe. In Belgium, a national acoustic receiver network for fish tracking was set up in 2014 with different research institutes collaborating. It is a permanent network with 163 acoustic receivers and since the start, over 800 animals from 14 different fish species have been tagged and generated more than 14 million detections so far. To handle all the (meta)data generated, a data management platform was built. The central database stores all the data and has an interactive web interface

that allows the users to upload, manage and explore (meta)data. In addition, the database is linked to an R-shiny application to allow the user to visualize and download the detection data. The permanent tracking network is not only a collaborative platform for exchange of data, analysis tools, devices and knowledge. It also creates opportunities to perform feasibility studies and PhD studies in a cost-efficient way. The Belgian tracking network is a first step toward a Pan-European aquatic tracking network.

2.3.2 Background

Telemetry is an increasingly applied method to investigate the behavioural ecology of aquatic animals in the wild. Multiple biotelemetry techniques are available to track aquatic animals and generate detailed spatiotemporal observations of their movements (e.g. dispersion, migration and homing) and habitat use. This information is needed to understand ecosystem functioning and dynamics. The biotelemetry techniques have already proven to provide cost-efficient crucial oceanographic data (Block et al. 2016), help in assessing the effects of anthropogenic disturbance by, for instance, man-made constructions (Reubens et al., 2014; Verhelst et al., 2018c; Winter et al., 2010) and thus deliver the necessary insights for efficiently managing, restoring and conserving aquatic species and habitats (Abecasis et al., 2014; Afonso et al., 2016). The resulting data and knowledge form the scientific basis of international policies and directives for species and habitat conservation (Hussey et al., 2015; Lennox et al., 2017), such as the Common Fisheries Policy and the Integrated Maritime Policy, Natura 2000, Marine Strategy Framework Directive and the Water Framework Directive, among others.

Aquatic systems are highly interconnected, linking different environments to one another and enable species to move over large distances, crossing administrative borders. This has triggered the development of large scale regional, national and international tracking network initiatives around the globe (e.g. IMOS Animal Tracking in Australia (Steckenreuter et al. 2016), OTN in Canada (Whoriskey and Hindell, 2016) and ATN in the United States (Block et al., 2016)). Each network not only entails the development and maintenance of physical networks of devices, but also the set-up of collaborative platforms for data exchange, analysis tools, devices and knowledge. Clearly, these coordinated, large scale and integrated approaches offer the users valuable opportunities to: 1) scale-up the study area and questions at stake by improving data gathering and sharing among stakeholders; 2) increase funding opportunities and; 3) encourage industry commitment to ensure compatibility between brands and technologies (Hussey et al., 2015; Lennox et al., 2017). In Belgium, scientists collaborated in the set-up of a permanent acoustic receiver network for fish tracking, by merging several local networks of smaller fish tracking projects of different institutes. Here we discuss the rationale behind the network, the current status and data-flow, the opportunities and the integration in a European tracking network.

2.3.3 The Belgian tracking network

Rationale

The Belgian tracking network resulted from a collaboration between Ghent University, the Research Institute for Nature and Forest (INBO) and the

Flanders Marine Institute (VLIZ) in the framework of LifeWatch (<http://lifewatch.eu/>).

The LifeWatch consortium, which was established in 2012 as part of the European Strategy Forum on Research Infrastructure (ESFRI), works as a virtual laboratory and is meant to support biodiversity research, for climatological and environmental impact studies, to support the development of ecosystem services and to provide information for policy makers in Europe. This large European research infrastructure consists of several biodiversity observatories, databases, web services and modeling tools. It integrates the existing systems, upgrades them and develops new systems. Since 2017, LifeWatch is fully operational and will run for at least 20 years, aiming at long term series of observation data.

As part of the Belgian contribution to LifeWatch, a national marine-freshwater-terrestrial observatory was constructed (<http://www.lifewatch.be/>) (Fig. 2.3). Many kinds of devices for automated data gathering were installed. The acoustic receivers, used to track fish in their natural environment, are one type of devices. The Belgian tracking network includes the physical network of acoustic receivers and the data management system. The latter involves the database, the data portal and the data explorer.

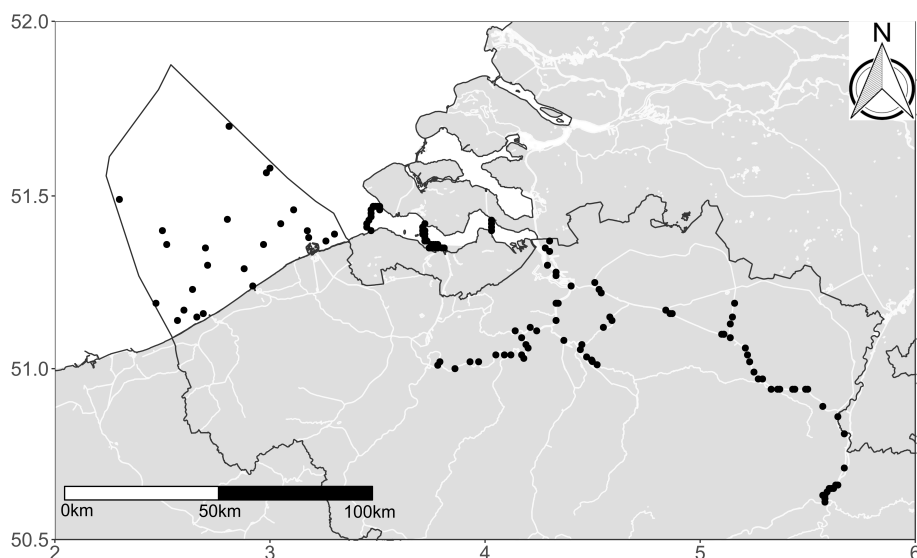


Figure 2.3: The Permanent Belgian Acoustic Receiver Network. Each dot represents a receiver station. National borders as well as the Belgian part of the North Sea are indicated with black solid lines and rivers with white solid lines.

The physical network

The Permanent Belgian Acoustic Receiver Network (PBARN) consists of 163 permanently installed receivers: 25 in the BPNS; 79 in the Schelde river basin (of which 39 in the Westerschelde, and 40 in the Zeeschelde, Nete, Rupel and Dijle), 43 in the Albert Canal and 16 in the Meuse river. The coverage of the permanent network allows tracking of fresh water, marine and diadromous fish in different environments, which are in a greater or lesser extent regulated

by human activities. Studies on the permanent network involve PhD studies as well as government or internationally funded projects. The PBARN is, in times, extended by temporary receiver networks. These networks are deployed in the framework of specific projects or studies with a more local focus (e.g. a wind farm, a river stretch, a marsh area). In these projects higher resolution data or additional environments/geographic areas are required for the questions at stake. The number of receiver stations in the temporary projects, and the duration of their deployments depend on the project outline and duration. This manuscript uses the permanent network.

Different types of acoustic receivers of VEMCO Ltd (Canada) are used (i.e. VR2W, VR2Tx, VR2C and VR2AR) and the type depends upon the environment and mooring opportunities. Receivers are moored on navigation buoys, ship wrecks, man-made structures (i.e. reefballs, wind turbines and shipping locks) and along river and canal banks. When attached to buoys, the receivers' hydrophones point downward. When attached to river or canal banks, the receivers are moored near the bottom in upward position. Depending on the type of mooring, the environment and the oceanographic and meteorological conditions, the detection probability of the receivers will differ. We refer to (Reubens et al., 2018) for detailed information on this issue.

Since the start of the network in 2014 over 800 animals have been tagged (Fig. 2.3). In total 767 animals of 13 species have been detected: 166 Atlantic cod (*Gadus morhua* L.), 95 Atlantic salmon (*Salmo salar* L.), 2 common carp (*Cyprinus carpio* L.), 4 common dab (*Limanda limanda* G.), 3 European chub (*Squalius cephalus* L.), 392 European eel, 8 European flounder (*Platichthys flesus* L.), 3 European plaice (*Pleuronectes platessa* L.), 1 lemon sole (*Microstomus kitt* W.), 30

river lamprey (*Lampetra fluviatilis* L.), 2 sea lamprey (*Petromyzon marinus* L.), 35 Twaite shad (*Alosa fallax* L.), 6 common roach (*Rutilus rutilus* L.) and 20 welsh catfish (*Silurus glanis* B.). Several eels from acoustic telemetry projects in The Netherlands and Germany have been detected on the PBARN (Huisman et al., 2016), which explains the higher number of observed versus tagged eels.

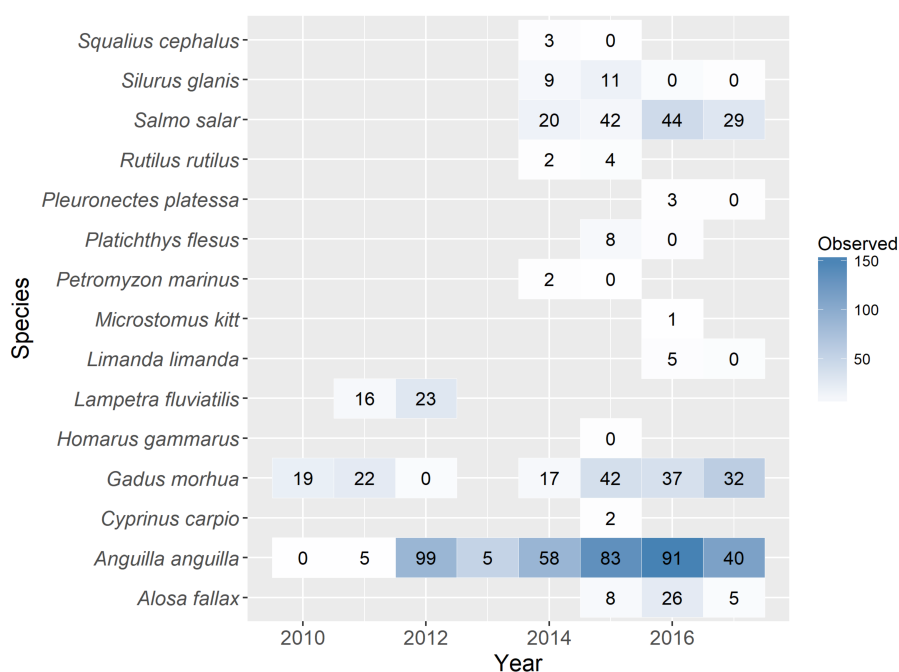


Figure 2.4: Information on tagged species. The numbers indicate the number of tagged individuals per species and per year. The colour gradient indicates the number of individuals per species and per year detected by the Belgian acoustic receiver network.

So far, the PBARN generated more than 14 million detections. Most of these

detections occurred at receiver stations in the rivers, canals and the Westerschelde estuary (Fig.2.5). This is, however, strongly correlated to the tagging location and number of specimens per species tagged. The BPNS on the other hand had most of the occurrences from eels tagged abroad (Huisman et al. 2016). These results indicate that each part of the PBARN renders valuable information.

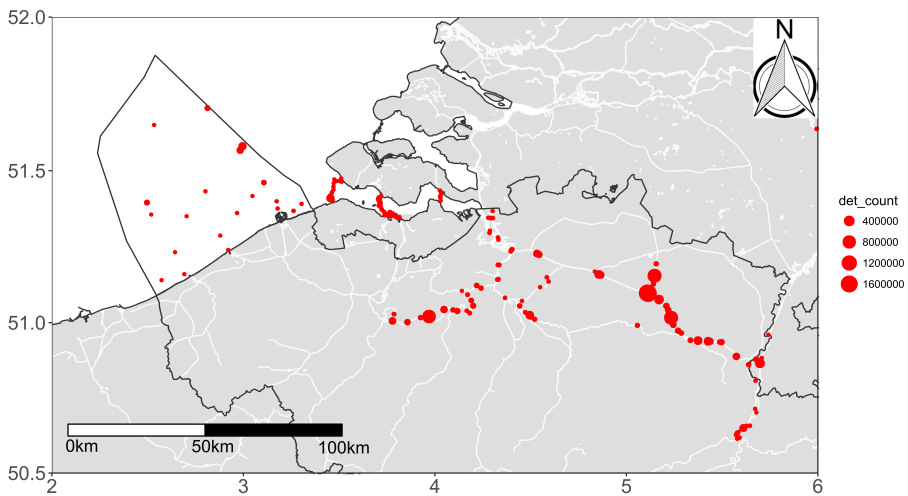


Figure 2.5: Indication of the locations where species have been detected. Size of the dots indicate the number of detections that occurred at that station.

Data management

Next to a physical network, proper data management is needed for a successful telemetry network. All data are stored in a central PostgreSQL database hosted by VLIZ. The database stores both the occurrences (i.e. detection data) and the metadata related to tags, animals, receivers, deployments and projects. An interactive online web interface (<http://www.lifewatch.be/etn>), developed in PHP using Symfony framework, gives access to all detection- and metadata stored in the database and allows to manage and explore it. Upload of the detection and metadata into the database occurs in a semi-automated way. Several quality controls, to minimize the chance on human errors and maximize the data quality, are performed on the data. There is a data policy (see <http://www.lifewatch.be/etn>) with moratorium rules in place to ensure that 1) data ownership is protected and 2) data becomes open access to the public at large after the moratorium period ended. We refer to the manual (<http://www.lifewatch.be/etn/assets/docs/ETN-DataManual.pdf?1.0>) for detailed information about the data management platform.

To explore, visualize and download the detection data an R Shiny application was developed (<http://rshiny.lifewatch.be/ETNdata/>).

Opportunities

In addition to the advantages mentioned in section 1, the PBARN has proven to create opportunities. One of these is the ability to perform a feasibility study in a cost-efficient way. For some species it is difficult to assess whether acoustic telemetry will be the most suitable technique for a specific research question.

With the presence of a network, a feasibility study can be performed with a limited number of acoustic tags. Such a study can render information on the type and amount of data that will be gathered, and on the geographical and temporal coverage. This can also aid researchers to decide on number of receivers and tags needed and to place receivers at strategic points to maximize detection of the species of interest. Breine et al. (2017) for instance, could test a modified external tagging technique on twaite shad. Shads are very sensitive to handling and stress, rendering the species rather unsuitable for electronic tagging studies. However, the authors of this study succeeded in the development of an external attachment procedure for twaite shad. Through the availability of an extensive array of receivers in the Schelde Estuary, this study could be performed with a limited amount of resources. Further, several pilot studies, which will use the PBARN, are currently initiated for European sea bass (*Dicentrarchus labrax* L.) and starry smooth-hound (*Mustelus asterias* C.). Similarly to pilot studies, the existence of the permanent network can aid PhD studies, as the resources for PhDs are often limited to a bench fee that does not allow to cover the equipment and logistics needed for large experimental set-ups. The PBARN reduces the equipment needs and costs related to logistics and maintenance. Three PhD studies, making use of the BARN, are currently ongoing : two on European eel (Huisman et al., 2016; Verhelst et al., 2018a,b,c,d) and one on Atlantic cod.

Next to providing infrastructure, a coordinated network also stimulates cooperation between researchers on national and international level. In 2014 and 2015, European eels from different river catchments in Western Europe (i.e. Belgium, The Netherlands and Germany) were detected on the PBARN. So far, it was assumed eels use the Nordic migration route over Scotland. However,

these detections revealed that at least a part of the population uses another route. Although the different studies were independently organized and focused on different research questions, it resulted in a peer-reviewed publication (Huisman et al., 2016), describing this novel insight in eel spawning migration. Another ongoing study on silver eel escapement in The Netherlands resulted, once again, in detections on the PBARN.

Further, not only infrastructure and data, but also expertise can be exchanged. Telemetry experts from Belgium are currently involved in several projects in The Netherlands and Germany to train their colleagues (unpublished data).

2.3.4 Towards a European Tracking Network

The PBARN is a national showcase proving the value of coordinated networks. However, this national network is just a first step towards a larger, international aquatic telemetry network. Several large scale initiatives are already active in different parts of the world (e.g. IMOS Animal Tracking in Australia, OTN in Canada, ATAP in South-Africa and GLATOS in the Great Lakes) (Cooke et al., 2011; Cowley et al., 2017; Hoenner et al., 2018). These networks address crucial scientific, conservation and management questions on a larger scale.

So far, Europe was lagging behind in these large-scale initiatives. To meet the demand for a Pan-European aquatic telemetry network, the European Tracking Network (ETN) was launched in 2017 in the framework of the European project AtlantOS (<https://www.atlantos-h2020.eu/>) (Abecasis et al.,

2018).

The data management system developed for PBARN will be used as the central data repository for ETN (<http://www.lifewatch.be/etn>). The necessary adaptations and extensions, required to cover European needs, were implemented recently and the system can now handle large amounts of data. With ETN, Europe will be positioned in the global arena of already existing aquatic telemetry network initiatives (Abecasis et al., 2018).

2.4 Methodological limitations

Obviously, acoustic telemetry has certain constraints, the detection probability being the most important one. The detection probability is highly variable depending on the system with a stable environment leading to a more constant detection probability. However, in dynamic systems such as estuaries and the marine environment, detection probability can vary substantially depending on the environmental conditions (Section 2.5). Also, the geomorphology of the system can have a serious impact on the detection probability. In the Albert Canal for instance, fish were detected over a distance > 1 km, likely attributed to the transmitter signals being scattered over large distances against the concrete embankments (INBO unpublished data). Another constraint of acoustic telemetry is the dependency on detection stations. When there are no mooring opportunities (i.e. no physical structures for attachment or administrative permission), no ALS can be deployed. In freshwater systems this is often not a big problem, but it is logistically impossible to cover large surfaces such as the Belgian part of the North Sea (BPNS). Yet, technological improvements such as

built-in acoustic releases allow more flexibility when no fixed mooring opportunities are present. Moreover, even with a sparse network leading to a low number of detections, important results can still be obtained (Chapter 8).

2.5 Environmental factors influence the detection probability in acoustic telemetry in a marine environment: results from a new setup

Published as: Reubens, J.; Verhelst, P.; van der Knaap, I.; Deneudt, K.; Moens, T.; Hernandez, F. 2018. Environmental factors influence the detection probability in acoustic telemetry in a marine environment: results from a new setup. *Hydrobiologia*: 1 - 14.

For the supplemental material, we refer to the online version of the article: <https://doi.org/10.1007/s10750-017-3478-7>

P. Verhelst contributed to the data analysis, generating the figures and writing the text.

2.5.1 Abstract

Acoustic telemetry is a commonly applied method to investigate the ecology of marine animals and provides a scientific basis for management and conservation. Crucial insight in animal behaviour and ecosystem functioning and dynamics is gained through acoustic receiver networks that are established in many different environments around the globe. The main limitation to this technique is the ability of the receivers to detect the signals from tagged anim-

als present in the nearby area. To interpret acoustic data correctly, understanding influencing factors on the detection probability is critical. Therefore, range test studies are an essential part of acoustic telemetry research. Here, we investigated whether specific environmental factors (i.e. wind, currents, waves, background noise, receiver tilt and azimuth) influence the receiver detection probability for a permanent acoustic receiver network in Belgium. Noise and wind speed in relation to distance, the interaction of receiver tilt and azimuth, and current speed were the most influential variables affecting the detection probability in this environment. The study indicated that there is high detection probability up to a distance of circa 200 m. A new setup, making use of features that render valuable information for data analysis and interpretation, was tested and revealed general applicability.

2.5.2 Introduction

The use of acoustic telemetry has been growing a lot in recent years and acoustic receiver networks are being established around the globe in many different aquatic environments. Consequently, our understanding of the ecosystem functioning and dynamics (e.g. migration routes, spatio-temporal habitat use and movement behaviour of key species) in these environments has significantly improved in recent years. This knowledge provides a scientific basis for fisheries management (Hussey et al. 2016), species conservation, marine spatial planning (Abecasis et al., 2014; Afonso et al., 2016) and environmental impact assessment (Reubens et al., 2014; Winter et al., 2010). In 2014, a permanent acoustic receiver network was set up in the Belgian part of the North Sea (BPNS), the Westerschelde (The Netherlands) and several rivers and canals

in Belgium in the framework of a long-term European project 'LifeWatch' that aims at automated monitoring of biodiversity (<http://www.lifewatch.be>). The Belgian network currently consists of 177 receiver stations in the marine, estuarine and freshwater environment (Fig. 2.6). It is a dynamic network and receiver stations can be added or removed according to the requirements of the projects involved (see <http://www.lifewatch.be/etn/login> for the most recent update of the network). Such a network of receivers allows detailed observations of animal movement and behaviour in the aquatic environment.

Although acoustic telemetry is a cost- and labour-efficient method able to generate extensive datasets in a short time period, it also suffers some limitations (Gjelland and Hedger, 2013; Hobday and Pincock, 2011; Kessel et al., 2014) which are often less understood (Huveneers et al., 2016) or not taken into account. The most important limitation is related to the ability of a receiver to detect the signals from tagged animals in its vicinity. This so-called detection probability depends on many factors, which are linked to the physical characteristics of sound propagation through the water column (Gjelland and Hedger, 2017; Medwin and Clay, 1997), and can change over space and time. As a consequence, the successful application of acoustic telemetry and the correct interpretation of detection and movement data depend upon proper knowledge of the detection range (i.e. the relationship between detection probability and the distance between the receiver and tag) (Gjelland and Hedger, 2017; Kessel et al., 2014). It is therefore important to know the environment one is working in and the factors that could influence the applicability of the technique. Therefore, before a study is initiated, the applicability of receiver arrays or networks to the questions at stake should be carefully reviewed. Thus, extensive range tests should be performed. The results of such range tests can

be used to improve the setup and the design of the receiver arrays and/or to adapt the questions that can be answered (Hayden et al., 2016; Hobday and Pincock, 2011; Kessel et al., 2014; Selby et al., 2016; Steckenreuter et al., 2017; Stocks et al., 2014).

It is well known that the detection probability will depend upon several factors related to transmission parameters (frequency, signal strength) and sound attenuation properties in the water (absorption, scattering, spreading and reflection). These attenuation properties depend upon specific characteristics of the water mass and the geomorphology of the system (e.g. temperature, salinity, substrate type, vegetation, suspended particulate matter) (Gjelland and Hedger, 2017; How and de Lestang, 2012; Jensen et al., 2000; Kessel et al., 2014). In addition, both anthropogenic and natural sound sources may mask the signal as the signal-to-noise ratio becomes too low (de Jong et al., 2011; Huveneers et al., 2016). The BPNS, for instance, is a shallow ocean basin with sandy sediments and strong tidal currents and winds (Baeye et al., 2013; Fettweis et al.). In addition, intensive shipping traffic and offshore industry result in high anthropogenic noise generation (e.g. dredging and disposal, deepening of navigation channels, offshore wind farm construction) (Douvere et al., 2007). Both the environmental characteristics and the anthropogenic noise generation can influence the detection probability within the acoustic receiver network present in the BPNS.

Range tests can be performed in many different ways. Several options are available for the setup and duration of the test. Most used setups (a) are in situ, short term (i.e. a couple of hours to one day) range tests performed during the study, and (b) use a setup with single tags at different distances from a fixed re-

ceiver. We refer to Kessel et al. (2014) for an extensive literature review on this topic. In this study, a new setup was applied, which has the advantage that it tests detection probabilities over a prolonged period of time at fixed distances, using a multitude of sentinel tags. VR2AR receivers (VEMCO Ltd, Canada) were used. These receivers contain a hydrophone to record detections, a built-in transmitter which renders information on the exact transmission times, an acoustic release, and several sensors which monitor tilt angle, temperature, depth and noise. The tilt sensor is the most interesting sensor in relation to range tests as it gives an indication of the receiver angle. The latter may have a profound influence on the detection probability through the angle between the incoming sound wave and the hydrophone (Bergé et al., 2012), as well as through potential shadowing by the receiver body or the mooring frame. In addition, it is expected that different meteorological and oceanographic variables influence the receivers' detection probability through time.

In this study we assess whether specific environmental factors influence the performance of acoustic receivers in a part of the Belgian receiver network (Fig. 2.6). More specifically, we assess 1) the influence of wind, currents, waves, background noise, receiver tilt, azimuth and distance on the detection probability; and 2) the average detection range in this environment. In addition, the applicability of the new setup for range tests is evaluated.

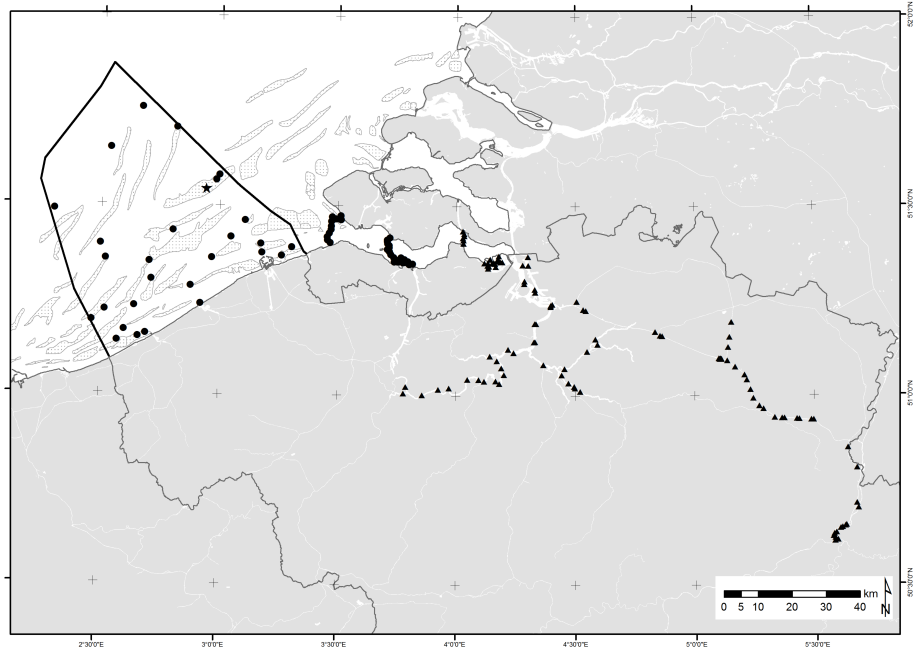


Figure 2.6: The Belgian acoustic telemetry network. The dots and triangles represent the 177 receiver stations currently in operation; the dots are those stations to which the results of the range test are assumed to be applicable; the black star indicates the location of the range test study. Bold black line delimits the BPNS, light-grey shading represents sand banks.

2.5.3 Material and methods

Study area

The study was performed at an offshore wind farm in the BPNS (Fig. 2.6). It is situated on the Thornton bank, a natural sandbank about 27 km off the Belgian

coast. The sandbanks in the BPNS are created by the strong tidal actions, which also results in a high turbidity (Otto et al., 1990). Water depth varies between 18 and 24 m in the area and the substratum consists of medium sand (Reubens et al., 2014). This site was specifically chosen as it is closed for all types of fishing, which effectively protects the receivers against bottom disturbance due to trawling activity and thus against damage and loss. The site represents typical conditions in the BPNS (i.e. shallow depths, sandy sediments and high current velocities). Thus, although the study was performed in a small area, it is assumed that the results are applicable to most of the network's receivers in the BPNS and the entrance of the Westerschelde (black dots in Fig. 2.6), except for receivers positioned in the freshwater-salt water transition area, where boundary transitions may have a profound additional effect on detection probability.

Study design and data collection

Deployment of receivers

Seven VR2AR acoustic receivers of VEMCO Ltd (Canada) were used. These receivers have a built-in transmitter (with several transmission power and delay options), sensors that measure tilt, depth, temperature and noise, and an acoustic release. These features make them favourable for range tests. The receivers recognize the tag IDs from the transmitters and log the detections together with a timestamp. The receivers were deployed at fixed distances, spaced between 50 and 350 meters from one another (Fig. 2.7). This setup results in 49 distances (i.e. 7 receivers each with 7 distances), ranging from zero (logs of built-in tags) to nearly 700 m, with approximately 50 m increments between the receivers and the transmitters (Fig. 2.7). Exact distances were based on GPS positions

taken during deployment (ranging from 0 to 683 m, see also Table 2.1). Transmission power of the built-in transmitters was set at 148 dB, with a random transmission delay between 60 and 120 seconds to avoid signal collisions.

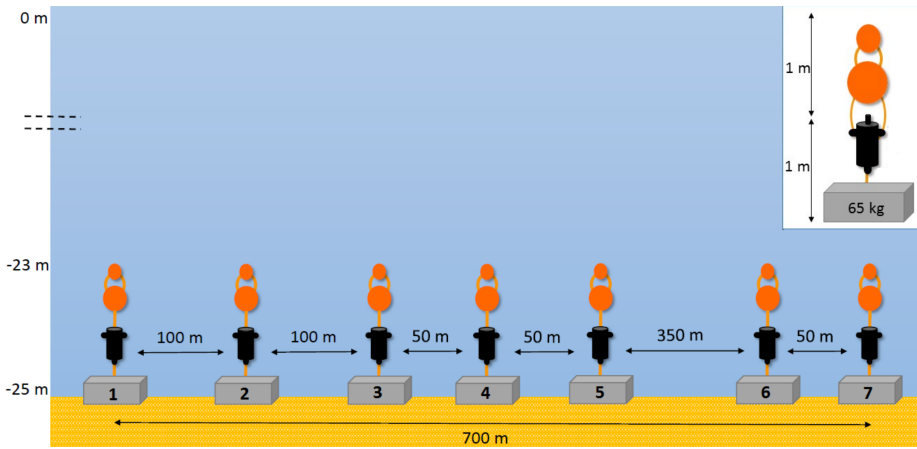


Figure 2.7: Setup of the range test. Seven acoustic receivers with a built-in transmitter were used. Distances range between 0 and 700 m, with 50 m increments. Tidal influence on depth is not taken into account.

The receivers were moored on the sea bottom with a block of bluestone of approximately 65 kg. Two hard plastic floats (280 and 180 mm diameter) were connected with polypropylene rope to the receiver to keep it in upright position (hydrophones pointing to the surface). Floats were positioned ca 1 m above the hydrophone to ensure that the detection field of the hydrophones was not blocked. No surface floats were used to avoid ship collisions. For detailed information on mooring design, see Vemco (2016a).

Table 2.1: Distance matrix (in meter) between receivers and built-in tags.

	R1	R2	R3	R4	R5	R6	R7
T1	0	85	176	232	281	631	683
T2		0	97	150	199	548	600
T3			0	59	106	455	507
T4				0	49	399	451
T5					0	350	402
T6						0	52
T7							0

Monitoring environmental parameters

Several oceanographic (current speed, current direction and wave height) and meteorological (wind speed and wind direction) parameters were measured during the study. Wind speed and wind direction data were obtained from 'Meetnet Vlaamse Banken', from station MOW 0 (51.33° N, 3.22° E) at 31 km from the study area. Wave height was also obtained by 'Meetnet Vlaamse Banken' but from station Westhinder (51.38° N, 2.44° E) at 39 km distance, as this data was not available at MOW 0. Current data was calculated from a 2D hydrodynamic model from the Operational Directorate Nature of the Royal Belgian Institute for Natural Sciences. The modelled currents are based upon astronomical tides and meteorological influences (i.e. wind and atmospheric pressure). In addition to these measured and modelled environmental para-

meters, the tilt measurements from the VR2AR built-in sensor were used as well. Although tilt is not an environmental parameter, it may potentially influence detection probability if this is not perfectly omnidirectional, and was therefore taken into account. This parameter was logged for the duration of the study with a ten-minute interval.

In addition, we calculated the azimuth (i.e. the angle) between the transmitter-to-receiver bearing and the current direction, scaled to 180° . This parameter provides additional information related to the angle between the receiver and the incoming signal, which may reveal e.g. shadowing effects caused by the receiver body. An azimuth of 0° indicates that transmitter-to-receiver bearing and current direction have the same bearing, while at 180° they have a completely opposite direction.

Temperature, salinity, depth and sediment type were not taken into account for the modelling, as receivers and tags were all present in the same environment and at very similar depths. No thermoclines nor haloclines are present in the area as the water column is well mixed.

The study ran for 22 days (from 18-02-2016 to 10-03-2016). This period encompassed varying environmental conditions (Table 2.2), making it possible to assess the influence of the different parameters on receiver performance and detection probability. Temperature varied between 6.5 and 8.0°C and average water depth was 23 m. Wind speed varied between 0.25 and 21 m s^{-1} , while current speed ranged between 0.13 and 0.92 m s^{-1} . Wave height varied between 0.30 and 2.54 m, tilt between 0 and 25° . The study was performed in winter time, allowing for harsh environmental conditions (i.e. strong winds and high waves).

Table 2.2: Minimum and maximum value of the different environmental parameters and the tilt. An overview of the different data collection methods and stations is provided.

Variable	Method	Station	Min. value	Max. value
Wind speed (m s^{-1})	Measured	MOW 0	0.25	20.95
Wind direction($^{\circ}$)	Measured	MOW 0	0.14	359
Current speed (m s^{-1})	Modelled	/	0.13	0.92
Current direction ($^{\circ}$)	Modelled	/	0.07	359
Wave height (cm)	Measured	Westhinder	30	254
Tilt ($^{\circ}$)	Measured	Built-in sensor	0	25
Noise (mV)	Measured	Built-in sensor	105	903

Data analysis

At the end of the study, data was downloaded from the receivers and was uploaded into the European Tracking Network database (<http://www.lifewatch.be/etn>). A dataset, containing the 442,856 transmissions from the built-in transmitters detected by the seven receivers, was created.

Detection data were binned per half hour (as the weakest resolution of the environmental data was per half hour) for each receiver-tag combination (hereafter referred to as events), and linked to the environmental parameters for the same time period. All events in which no detections were encountered were also added to the data frame, as we were not only interested in pres-

ences, but also absences. This resulted in 49,098 distinct events. As receiver clocks are sensitive to time drift, detection data were accounted for possible time drift using the linear time drift correction available in the VUE software of VEMCO Ltd. It was assured that PC clock time was correct at the moment of initialization of the receiver and upload of the data. The effects of the environmental variables on the detection probability were assessed. First, the data were checked for outliers (defined as data points below $Q1 - 1.5 \times IQR$ or above $Q3 + 1.5 \times IQR$) followed by a collinearity analysis (Zuur et al., 2010). If correlations were found, one of the covariates was excluded from the analysis (Dormann et al., 2013).

To determine which environmental variables contributed to the detection probability, a generalized linear model was applied. The covariates were scaled by applying a z-transformation:

$$x = \frac{x - \text{mean}(x)}{\text{sd}(x)}$$

The model was tested for overdispersion and zero-inflation. Overdispersion was tested using the vuong test from the pscl package in R (R Development Core Team 2017). As the vuong test revealed that the negative binomial distribution performed better than the Poisson distribution, it could be assumed that overdispersion did occur and thus the negative binomial distribution should be used. A histogram showing the number of detections per event revealed that the data were zero-inflated. Due to the random transmission delay of the tags, the number of transmissions a tag emitted per half hour time bin differed through time. To account for this, an offset was used in the model (Zuur et al., 2009). The offset was defined as the logarithm of the num-

ber of transmissions sent out by the built-in tag per event. Based on the result from the above tests, it was decided to use a zero-inflated negative binomial (ZINB) distribution with an offset for the model development. For more details on ZINB models we refer to Zuur et al. (2009). The package `pscl` of the R environment (R Development Core Team 2017) was used. Based on Forstmeier and Schielzeth (2011) and Hegyi and Garamszegi (2011) it was decided to work with the full model.

In addition, to estimate the average detection range within our study site, the detection probability per distance was calculated for the half hour time bins. This probability was calculated as the number of transmissions received, divided by the number of transmissions sent out.

2.5.4 Results

Variables influencing detection probability

The large temporal variation in detection rate (Fig. 2.8) indicates that environmental factors influence the detection probability. Under favourable oceanographic conditions, transmissions can be received much further (even beyond 400 m). On the other hand, in unfavourable conditions, transmissions can be missed even at very close distances. Collinearity analysis revealed a high correlation between wave height and wind speed (0.72). We decided to remove wave height since wind information consists of two components (direction and speed), each of which can be informative. The model revealed that several environmental parameters influence the detection probability. The interactions of noise and distance, and of wind and distance contributed most, followed

by the interaction between tilt and azimuth, and current speed (Table 2.3). It should be kept in mind that there still is a lot of unexplained variation. At close distances, the detection probability is not much influenced by noise or wind. However, at larger distances, noise and wind negatively influenced the detection probability (Fig. 2.9, Fig. S2). The influence of the azimuth depended upon the receiver tilt. At no or low receiver inclination, the detection probability increased with increasing azimuth; while at higher receiver inclination, azimuth negatively influenced the probability. The detection probability decreased only slightly between minimum and maximum current speed (Fig. 2.9), hence the current speed only has a limited impact on the detection probability.

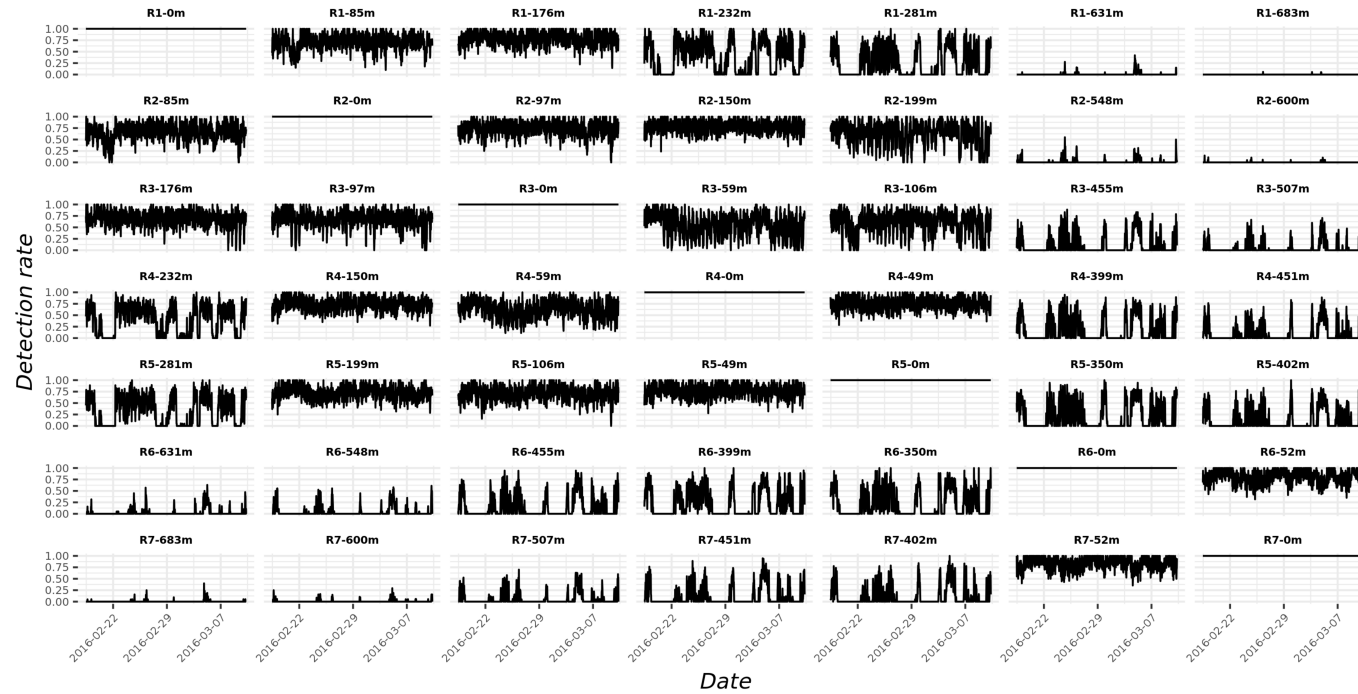


Figure 2.8: Detection rate for all distances for the seven groups for the duration of the study. Each group represents the detections over time of one receiver linked to seven transmitters.

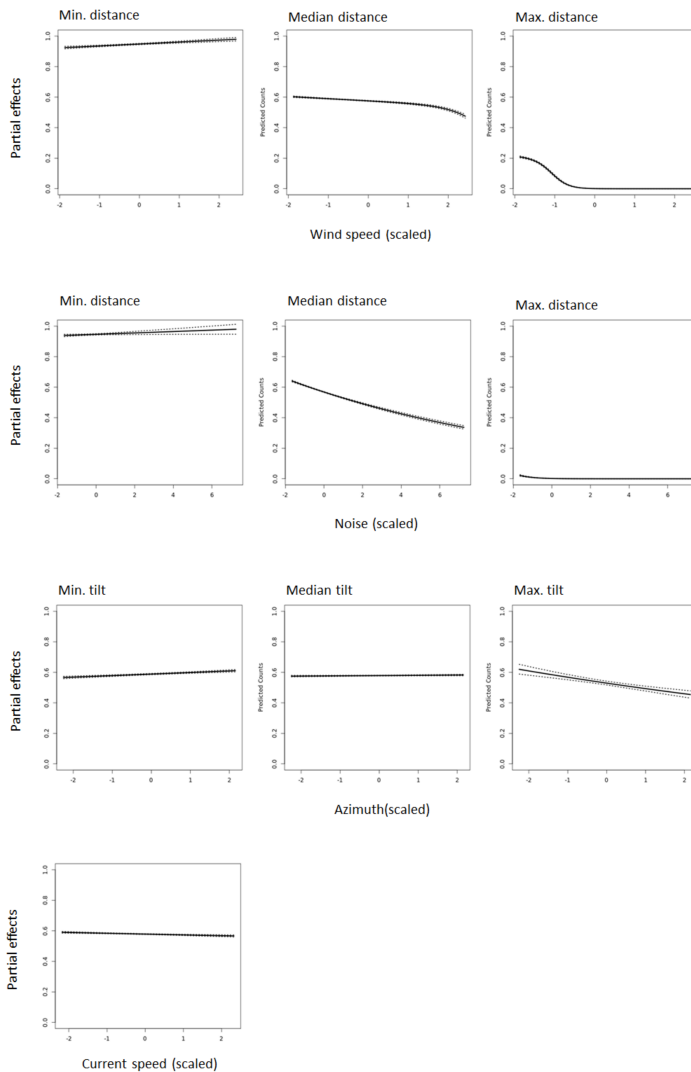


Figure 2.9: Summary of the partial effects of the environmental parameters on the detection probability. For interaction effects, the minimum medium and maximum value for distance and tilt are shown. Dashed lines indicate the 95% confidence intervals.

Table 2.3: Zero-inflated Poisson model summary.

	Estimate	SE	z value	p-value
Count part: <i>Negbin with log link</i>				
Intercept	-0.75	0.00	-211.95	< 0.001
Wind speed	-0.04	0.00	-10.05	< 0.001
Distance	-0.57	0.00	-149.79	< 0.001
Wind direction	-0.01	0.00	-4.07	< 0.001
Tilt	-0.02	0.00	-7.21	< 0.001
Azimuth	0.00	0.00	-0.81	0.42
Noise	-0.10	0.00	-32.83	< 0.001
Current speed	-0.01	0.00	-4.25	< 0.001
Current direction	0.00	0.00	0.64	0.52
Wind speed*Distance	-0.04	0.00	-10.69	< 0.001
Tilt*Azimuth	-0.01	0.00	-7.14	< 0.001
Noise*Distance	-0.08	0.00	-27.68	< 0.001
Log(theta)	13.63	9.54	1.43	0.15
Inflated part: <i>Binomial with logit link</i>				
Intercept	-5.15	0.04	-129.81	< 0.001
Wind speed	2.46	0.04	59.44	< 0.001
Distance	5.58	0.07	80.45	< 0.001
Wind direction	-0.04	0.02	-1.90	0.057
Tilt	0.34	0.03	10.51	< 0.001
Azimuth	-0.03	0.03	-0.99	0.32
Noise	0.29	0.03	8.31	< 0.001
Current speed	0.23	0.03	7.72	< 0.001
Current direction	0.03	0.02	1.44	0.15
Wind speed*Distance	1.24	0.04	29.17	< 0.001
Tilt*Azimuth	-0.05	0.04	-1.33	< 0.18
Noise*Distance	0.47	0.04	12.02	< 0.001

Detection range

Figures 2.8 and 2.10 reveal that the average detection probabilities are high (i.e. above 70%) until a distance of ca. 200 m, whereafter they quickly drop to (near) zero at a distance of 350 m. These results indicate that there is a limited detection range within this dynamic environment. However, there is considerable temporal variation in detection probability, and thus in detection range.

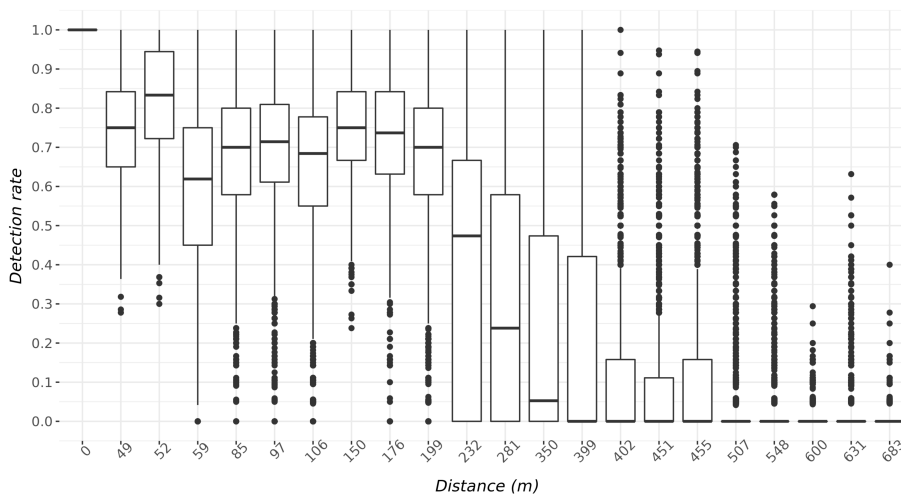


Figure 2.10: Boxplots of detection probability in relation to the distance between receiver and transmitter. Dots represent outliers.

2.5.5 Discussion

Variables influencing detection probability

Our results demonstrate that detection probability is not static and can change considerably over time. It was mainly influenced by noise and wind speed in relation to distance, the interaction between tilt and azimuth, and to current speed; which is in agreement with Gjelland and Hedger (2013); Huveneers et al. (2016). In contrast, Stocks et al. (2014) listed wave height as the principal factor affecting detection range. However, wave height was highly correlated with wind speed, hence our study does not contradict the results of Stocks et al. (2014).

The influence of wind can be attributed to both the noise generation itself and to the air bubbles that are mixed into the water column (Gjelland and Hedger, 2013). Scattering of signals in strongly wind-influenced surface layers will, due to air bubbles (Medwin and Clay, 1997) and multi-path (Dol et al., 2013), increase the sound attenuation in these layers, but also contribute to increased background noise levels, even at larger depth.

The interaction effects of noise with distance, and of wind with distance can be explained by the signal-to-noise ratio (SNR). At close distances, the SNR is still high, hence the transmitted signal strength dominates over the ambient noise (including wind-generated noise) present in the environment. At higher distances, the transmitted signal has already lost part of its strength due to attenuation and interference, and therefore negatively influences the SNR (Vemco, 2015).

The present study was performed in an offshore wind farm, and although it is expected that ambient noise in this area is lower than in the surrounding environment because no shipping or industrial activities take place here, noise still significantly influenced the detection probability. Both anthropogenic and natural sound sources may mask the transmission signal (de Jong et al., 2011; Gjelland and Hedger, 2017; Huveneers et al., 2016), and it is difficult to attribute the impact to a specific sound source. As the sound sources, and thus the SNR, strongly vary in both spatial and temporal context, the influence of noise on the detection probability may strongly differ between receiver stations in the Belgian network.

The influence of currents, on the other hand, can be attributed to both flow noise and tilt angle of the hydrophone. Flow noise refers to changes in pressure and the creation of eddies around the hydrophone under high flow conditions, and can be caused by movement of the hydrophone in the water column (Martin et al., 2013). In addition, the hydrophone can also receive strumming noise from ropes under tension. As flow noise generally occurs below 1 kHz (Martin et al., 2013), this does not cause problems for acoustic receivers. However, the eddy creation may cause sound attenuation. The tilt angle of the hydrophone presumably better explains the variation in the detection probability than current in itself (Fig. S3). The higher the current velocity, the higher the tilt angle becomes. If the tilt angle becomes too high, the hydrophone no longer has an unobstructed view and shadow zones are created (Vemco, 2016a), which can adversely affect the detection probability. However, this is also influenced by the azimuth as, the interaction effect between tilt and azimuth indicated. The azimuth is defined as the angle between the transmitter-to-receiver bearing and the current direction, which changes over time. At some moments

in time, the receiver may be tilted towards the focus transmitter, resulting in a higher detection probability. With changes in the current direction, the receiver is tilted away from the transmitter, causing reduced detection probability due to shadowing.

In addition, the present results reveal that the detection probability does not decline linearly, but shows some inconsistencies at close distances. Although the receiver-transmitter distance was within the same range between 49 and 59 m, the detection probability differed considerably. This might be related to small local differences in the environment, as mentioned earlier. However, it can also be related to close-proximity detection interference (CPDI) or tag code collision. As stated by Kessel et al. (2015) and Gjelland and Hedger (2017), CPDI occurs when reflective barriers (e.g. water surface, air bubbles) result in multiple pathways from transmitter to receiver. As these multipath signals have the same frequency, they contribute to the background noise. Code collision is a function of the number of transmitters within range of the receiver, the signal duration and signal delay (Binder et al., 2016). At larger distances there is a reduction in code collisions as transmissions are attenuated.

Besides environmental variables, sediment characteristics and topography, also the mooring design, the transmission characteristics of the tags, the transmitter attachment on the fish and the configuration of the receivers can all influence the detection probability (Clements et al., 2005; Dance et al., 2016; Heupel et al., 2006; Hobday and Pincock, 2011; Simpfendorfer et al., 2008). For this range test, transmission power output was set at 148 dB, and the receivers were moored near the bottom with the hydrophone pointing in an upward direction. Different setups or tag specifications will undoubtedly affect the

results. Many of the receivers deployed in the BPNS and the Westerschelde are moored near the surface (using navigation buoys) with the hydrophone pointing downward. As wind action significantly influences detection probability, it can be expected that receivers near the surface will be more negatively influenced by wind than receivers near the bottom. On the other hand, the range test was performed in winter, when more extreme weather events such as storms and high waves occur. In the whole of 2016, the maximum wind speed was 25 m s^{-1} at MOW 0, with a peak of 21 m s^{-1} during our test period, while the largest wave height measured in 2016 was 3.8 m, compared to 2.54 m during our test period. High wind speeds and wave heights were mainly measured in quarter 1 of 2016. As a result, most of the year, detection range may be higher than what we found in this study.

Detection range

The present study demonstrates that there is a good detection probability up to 200 m, but it quickly reduces beyond this distance. This detection range is in the range of previous reports, which encompass both higher (Hobday and Pincock, 2011; Huveneers et al., 2016) and similar range values (Cagua et al., 2013; Stocks et al., 2014; Welsh et al., 2012). Some other publications have reported a broad range of distances within the same study (Cagua et al., 2013; Gjelland and Hedger, 2013; How and de Lestang, 2012). Although the detection ranges differ extensively between the cited studies, they all concluded that detection range strongly depends upon meteorological and oceanographic environmental variables, on sediment characteristics, and on the environment's topographic complexity; factors which all influence sound propagation in wa-

ter. As environmental conditions and topography differ largely between areas, detection ranges will do so as well. Even in environments that look comparable at first sight, small local differences can have large effects on the detection probabilities and thus also on the detection ranges.

Coping with variation in detection probability

Of similar importance as knowing which factors influence the detection probability, is to know how to account for this variation in detection probability (Gjelland and Hedger, 2013, 2017). Performing adaptations at the level of data-analysis, mooring and receiver setup, and/or research questions can partly overcome the problem. Changes to the setup or the questions to be answered can only be made if there is some a priori knowledge on the influencing factors. On many occasions, influences on detection probability only become clear once data-analysis has started. This underlines the importance of reliable data analysis when dealing with the specific situation where the factors influencing the detection rate may bias the results towards false negatives (absences of recordings on specific moments despite fish being present). Data analysis should take this increased likelihood of false negatives into account. This can, for instance, be done by including a prevalence-adjusted performance criterion. Such a criterion contains an adjustable parameter that corrects for false negatives (Mouton et al., 2009a). The performance criterion can vary as a function of the influencing environmental parameters and thus allows incorporation of ecological relevance in the model optimisation process (Mouton et al., 2009b) to more accurately model the fish movement behaviour.

The present study revealed that current speed and azimuth influence the

detection probability. This indicates that the mooring design could be improved. By fixing the receiver (e.g. on a frame), the hydrophone wouldn't be able to tilt anymore. As a result, the 'line of sight' between receiver and transmitter wouldn't change in function of the current direction. Although not empirically tested, this would probably reduce the statistical noise in the data.

Applicability of the range test setup

In Belgium, several short-term (i.e. hours up to a few days) range tests have previously been undertaken (but were never published) in both marine and freshwater environments. The current study is the first extensive range test in Belgian offshore waters and the setup used has, to our knowledge, never been used before. The research field of acoustic telemetry is characterized by fast technological improvements and new developments are launched regularly (Whoriskey and Hindell, 2016). The VR2AR receivers used in this study are a relatively new type of receivers that combine a regular receiver with a built-in transmitter, an acoustic release, and several sensors which monitor tilt angle, temperature, depth and noise (Vemco, 2016b). There are several aspects that make such a type of receiver favourable for range testing. First, the transmission events from the built-in tag are logged in the memory of the receiver. They don't actually listen to their self-transmissions, but simply record the date and time that they transmitted, thus allowing the researcher to know the exact number of transmissions in a specific time period. This is a practical feature if the transmitters are programmed to send their signal in random delay modus or in situations where there is a high chance for echo detections due to the characteristics of the environment (e.g. in areas with hard substrates or ice

cover). Secondly, the available sensors give in-situ information on receiver tilt and an estimate of the presence of noise in the environment (Vemco, 2016b). Although it doesn't give detailed information, this data can already inform researchers about possible environmental features conflicting with the transmissions. Further, with a limited number of units, many different distances between receiver and tags can be created, resulting in detailed information on the relation between detection probability and distance. Lastly, the built-in acoustic release allows for easy retrieval, without the need for surface marker buoys. This reduces complexity of the setup, and thus considerably reduces the chance of recovery failure of the mooring.

2.5.6 Conclusion

When interpreting acoustic telemetry data, it is important to keep in mind how the characteristics of sound propagation through water relate to environmental factors (i.e. meteorological, oceanographic and topographic) and interfere with other sound sources (both natural and human). It is important that scientists understand these influencing factors, consider their contribution, and adjust for them where possible, when interpreting the results. We encourage performing range tests for each study area, and when possible, for the entire duration of a study. If the latter is not possible, the range test period should at least cover a time span that is sufficient to assess the influence of varying environmental conditions on detection probability.

The setup tested in this study made use of features (e.g. transmission event and tilt data) that render valuable information for data analysis and interpretation of the results. The setup is easy to deploy and retrieve. These aspects

make it a comprehensive technique with potential for general applicability.

Chapter 3

Movement behaviour of large female yellow European eel (*Anguilla anguilla* L.) in a freshwater polder area

Modified after:

Verhelst, P.; Reubens, J.; Pauwels, I.; Buysse, D.; Aelterman, B.; Hoey, S.; Goethals, P.; Moens, T.; Coeck, J.; Mouton, A. 2018. Movement behaviour of large female yellow European eel (*Anguilla anguilla* L.) in a freshwater polder area. *Ecology of Freshwater Fish* **27**: 471 - 480.

For the supplemental material and appendix, we refer to the online version of the article: <https://doi.org/10.1111/eff.12362>

3.1 Abstract

Due to a recruitment decline of more than 90% in 30 years, the European eel has been classified by IUCN as critically endangered. Although the species has been studied intensively to obtain knowledge to improve management, studies about the resident yellow stage are relatively scarce. In this study, 52 large female yellow eels were tagged with acoustic transmitters in a Belgian polder system and tracked by a network of 23 ALSs. We studied both circadian and seasonal movement patterns and the effect of environmental variables on these patterns. Large female yellow eels were most active at night in late summer and early autumn. A generalised linear mixed model showed that their movement is only slightly influenced by environmental variables. Moreover, as yellow eels show high site fidelity (i.e., the majority was detected only in the habitat type of their catch-release location), they do not encounter many human-induced connectivity problems in polder systems, which makes these systems highly suitable as eel growth habitat. These results can contribute to an effective eel management regarding habitat protection and restoration.

3.2 Introduction

Due to the endangered status of the European eel population, it is crucial that eel growth habitats obtain proper protection. Among suitable eel growth habitats, polders are anthropogenic water bodies where water levels are controlled by, for example, embankments, weirs and pumping stations to prevent flooding. Polders are characterised by a network of canals, connected ponds and

ditches, resulting in a high habitat diversity and thus many potential growth areas (Lasne et al., 2008). This could lead to higher growth rates, and larger eels have a higher survival rate (Boulenger et al., 2016). In addition, these areas are located close to the sea and may therefore, in the absence of migration barriers, be easily colonised by glass eels (Laffaille et al., 2004). Little is known about the importance of polders for eels, especially for yellow eels, which is the sedentary growing stage (Laffaille et al., 2005). However, due to climate change-driven sea-level rise (Nicholls and Cazenave, 2010), the polder area will tend to increase worldwide during the upcoming decades, turning these systems into potentially important eel habitat and interesting study areas.

Research on eel behaviour may provide insight into the importance of polder areas for yellow eel, especially because behaviour research has hitherto mainly focused on upstream migration during the glass and yellow eel stages and downstream migration during the silver eel stage (e.g., White and Knights (1997); Davidsen et al. (2011); Mouton et al. (2011a); Buysse et al. (2015); Nzau Matondo and Ovidio (2016)). While it has been reported that yellow eels may move seasonally (Jellyman and Sykes, 2003), are primarily nocturnal and that their activity increases with water temperature (Baras et al., 1998), substantial knowledge gaps still exist about the habitat utilisation and movement of yellow eels. It is, for instance, unknown to what extent eels move in a polder area, what is their movement range and whether they use different habitats within that range. It is also unknown what environmental variables trigger movement.

In this study, we investigated the behaviour of large female European eels in a polder area in Flanders, Belgium, by acoustic telemetry. Both yellow- and

silver-staged eels were tagged in this study. However, the classification of eels in yellow and silver stages is rather arbitrary (Durif et al., 2005), especially because silver eels can postpone their migration and turn into a semiyellow stage (Svedäng and Wickström, 1997). This study was based on resident (i.e., nonmigratory) behaviour, and as such, all tagged eels were female yellow eels, based on morphometric criteria (Durif et al., 2005; Laffaille et al., 2005). The main aims of this study were to investigate different aspects of yellow eel behaviour in a polder system. Specifically, we investigated (i) when yellow eels were most active in terms of circadian inter-ALS movements and seasonal swim distance patterns, including effects of temperature, (ii) the size of the movement range and (iii) what environmental variables determined movement. In addition, we checked for (iv) an effect of habitat type (i.e., canal, polder ditch and pond) on (ii) and (iii). A better understanding of yellow eel behaviour will contribute to effective polder management including habitat restoration and protection. Such measures may lead to a higher survival up to the silver eel stage and hence to a higher seaward escapement rate.

3.3 Methods

3.3.1 Study area

The study was performed in a polder area in Flanders, Belgium, which is part of the Schelde River Basin. The drainage area of the polder is ca. 200 km², and drainage is through the Leopold Canal (LC). During high precipitation, water is pumped from the LC into the Braakman pond via a pumping station in the

Isabella Canal (Boekhoute); it flows into the Schelde Estuary via a tidal sluice (Fig. 3.1). This is undoubtedly also the main migration route of silver eel from the polder to the estuary. The LC is an unnavigable waterway extending from the Belgian coast to Boekhoute. It is ca. 46 km long, 10–20 m wide and one to four metres deep. It is a stagnant water system, but during dewatering, the system can have a slow-flowing current (on average $1.21 \text{ m}^3 \text{ s}^{-1}$ during this study period). Connectivity from the polder area to marine areas is blocked by the weir in Sint-Laureins (except in cases of exceptionally high precipitation, when the system can be dewatered towards Zeebrugge by lowering a weir in the LC at Sint-Laureins) and the pumping station in Boekhoute (Fig. 3.1). The LC connects different habitats in the polder such as ponds and small and large polder ditches with variable width (0.5–150 m) and depth (0.2–10 m) (Table 3.1).

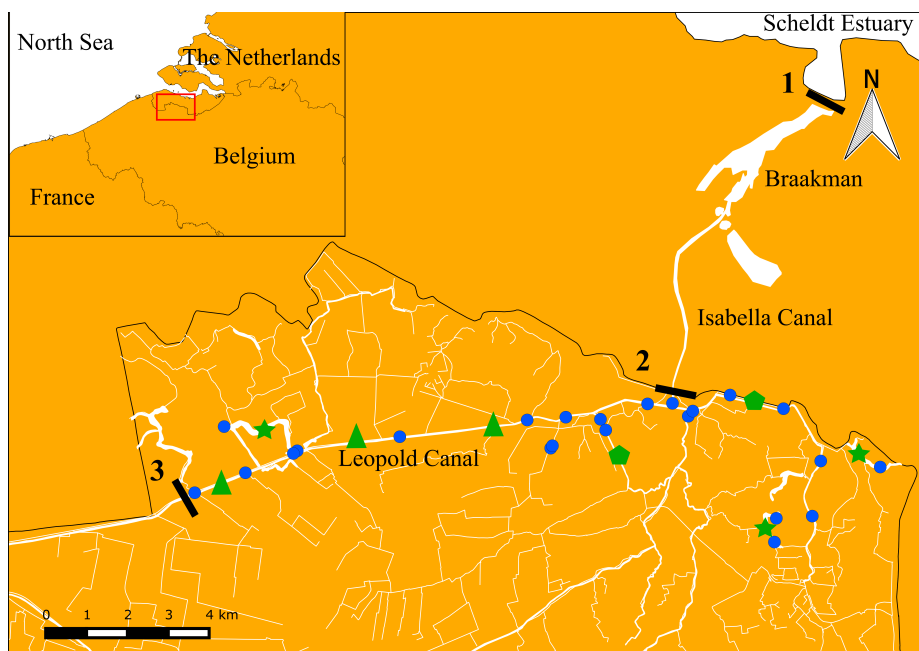


Figure 3.1: Study area with the location of the migration barriers and the network of waterways in the Belgian part of the polder area: (1) the tidal sluice, (2) the pumping station in the Isabella Canal (Boekhoute) and (3) the weir at Sint-Laureins. The blue dots represent acoustic listening stations, and the symbols are the different catch locations: ponds (star), Leopold Canal (triangle) and polder ditches (pentagon).

Table 3.1: Depth, width and current characteristics of the different habitat types.

Types	Depth (m)	Width (m)	Current
Canal	1 - 4	10 - 20	Slow
Pond	0.5 - 10	15 - 150	Stagnant
Large polder ditch	0.5 - 2	5 - 10	Slow
Small polder ditch	0.2 - 1	0.5 - 5	Slow

3.3.2 Tagging procedure

From July to August 2012, a total of 526 eels were caught with double fyke nets in the LC, ponds and large polder ditches (electrofishing in the small polder ditches did not yield any eels). At each location, four double fyke nets were placed and emptied for four consecutive days. Several morphometric features were measured in order to determine the sex and eel maturation stage according to (Durif et al., 2005): total length (TL, to the nearest mm), body weight (W, to the nearest g), the vertical and horizontal eye diameter (ED_v and ED_h respectively, to the nearest 0.1 mm) and the length of the pectoral fin (FL, to the nearest 0.1 mm). Fifty-two eels were considered large enough to tag, with a minimum TL of 495 mm and minimum weight of 246 g (Table S1). According to the size classes of Laffaille et al. (2003), the selected eels were considered large and female, as males are smaller than the minimum size handled in this study (<450 mm (Durif et al., 2005)) (Table 3.2). Five life stages can be found in

female European eel: a sexually undifferentiated growing phase (I), a female differentiated growing phase (FII), a premigratory phase (FIII) and two migratory phases (FIV and FV) (Durif et al., 2005). FIV-staged eels are considered to be on the onset of migration, while FV-staged eels are regarded as migrating eels. Here, yellow eel (FII, $n = 11$), premigrant eel (FIII, $n = 28$) and two classified migrant eel stages (FIV, $n = 4$, and FV, $n = 9$ respectively) were tagged.

Eels were tagged with V13-1L-coded acoustic transmitters (13×36 mm, weight in air 11 g, weight in water 6 g, random delay between 80 and 160 s, guaranteed life time 1,116 days, frequency 69 Hz) from VEMCO Ltd (Canada)). After anaesthetising the eels with 0.3 ml/L clove oil, tags were implanted according to Baras and Jeandrain (1998). After recovery in a quarantine reservoir, eels were released at their catch location.

Table 3.2: Number of tagged female eels per stage with the different morphometrics: total length (TL), body weight (BW), horizontal and vertical eye diameters (ED_h and ED_v respectively) and pectoral fin length (FL).

Stages	Number	TL (mm)	BW (g)	ED_h (mm)	ED_v (mm)	FL (mm)
FII	11	607 ± 32	392 ± 108	6.29 ± 0.46	5.96 ± 0.58	26.54 ± 1.78
FIII	28	662 ± 69	556 ± 190	7.59 ± 0.77	7.27 ± 0.75	31.96 ± 4.47
FIV	4	773 ± 81	$1,066 \pm 251$	9.74 ± 1.14	8.71 ± 1.17	36.07 ± 1.50
FV	9	630 ± 56	486 ± 123	9.16 ± 0.98	8.21 ± 1.20	33.58 ± 2.89

3.3.3 Acoustic network

An acoustic network of 23 ALSs (VR2W, VEMCO Ltd, Canada) was deployed in the polder system in the LC, Isabella Canal, ponds and large polder ditches. The ALSs register the tag IDs with date and time of the detections. They were moored at strategic locations (Fig. 3.1) to maximise the probability of detection and to minimise detection gaps: ALSs were deployed up- and downstream at each entry of a pond or polder ditch into the LC. In the pond and polder ditch itself, an ALS was placed near the connection with the LC and further upstream. They were on average 1,912 m (range 114-5,264 m) apart. The ALSs were moored at the bank by means of weights and a small buoy, so the ALS was deployed on the bottom with the hydrophone directed upwards in the water column. Data from ALSs were downloaded two to three times a year. As environmental conditions do not change drastically in the polder area, only a short-term range test (i.e., < 1 day) was performed. An ALS was moored in the different habitats in the polder and a range test tag [i.e., a tag with a very short fixed delay of ca. 10 s]) was positioned at several ranges (0-500 m, with 50-m intervals) from the ALS. Tests revealed detection ranges of 300 m.

3.3.4 Data processing

To determine residency times (time between arrival and departure at an ALS), searches were performed with the VUE software (VEMCO Users Environment, VEMCO Ltd, Canada). This allows us to reduce the data by accumulating the number of detections during a fixed period of time. We applied an absence threshold of 1 hr (i.e., the maximum time between detections within a single

residency period) and a detection threshold of one detection (i.e., the minimum number of detections required for a residency period). The residency search resulted in intervals with arrival and departure times per eel at each ALS. The numbers of detections between each arrival and departure per ALS were calculated. The residence time between arrival and departure, and the swim distance, swim time and swim speed between each consecutive interval were calculated in R (R Development Core Team 2017) .

Of the 52 tagged eels, 18 showed yellow eel (i.e., resident) behaviour followed by silver eel behaviour (i.e., migration: directional movements towards seawards exit from the polder system). As this study focused on yellow eel movement behaviour only, data on behaviour typical of silver eels were removed. To determine a clear distinction between yellow and silver eel behaviour, a trajectory analysis was applied for each individual eel. We used the method of Lavielle from the *adehabitatLT* package in R to divide an animal's trajectory into a yellow and a silver eel phase (Calenge, 2006) (Fig. S1). This method does not require discretisation in time and is based on residence time: it partitions movement segments based on homogeneous mean residence times (Lavielle, 1999, 2005; Barraquand and Benhamou, 2008). The 52 eels were detected as yellow eels between 4th July 2012 and 7th September 2015 (39 months), resulting in a data set of 1,627,846 detections; the average tracking period per eel was 470 days (range 28-1,135).

3.3.5 Data analysis

In this study, four research questions were addressed, each with its own data analysis. We investigated (i) when yellow eels were most active in terms of cir-

cadian inter-ALS movements and seasonal swim distance patterns, including effects of temperature, (ii) the size of the movement range, (iii) what environmental variables determined movement and (iv) effects of habitat type (i.e., canal, polder ditch and pond) on (ii) and (iii). For each analysis, assumptions were checked and data exploration was conducted following Zuur et al. (2010).

Circadian and seasonal activity

Circadian activity was defined as the total number of inter-ALS movements made by eels, as they moved between one ALS to an adjacent one per circadian phase. Consequently, four different circadian phases were determined and linked to each record in the data set: dawn (start of civil twilight to sunrise, i.e., when the geometric centre of the sun is 6° below the horizon in the morning (or evening for dusk)), day (sunrise to sunset), dusk (sunset to end of civil twilight) and night (end of civil twilight to start of civil twilight). Time stamps of sunset, sunrise and twilight were obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil/index.php>; coordinates: N51°16' E3°43').

Seasonal activity was analysed by summing the swim distances per eel for each month. Only data records of eels that swam to another ALS were taken into account. A one-way ANOVA with Welch correction was performed, as the variances were not homogenous. Following a significant ANOVA result, a Games-Howell post hoc test for multiple pairwise comparisons was applied (Games and Howell, 1976). The effect of water temperature on mean swim distance was analysed by means of a one-way ANOVA.

Movement range

Polder areas are geographically complex systems, where it is hard to apply classical methods of movement range estimation such as minimum convex polygons and kernel utilisation distribution (Benhamou and Cornélis, 2010; Heupel et al., 2004; Meyer and Holland, 2005). Moreover, the detection range of the ALSs deployed in the study area was larger than the width of the waterways. As such, the movement range was considered as the distance swum by an eel between the two most distant ALSs during the tracking period (Walker et al., 2014). Although some eels were only detected at one ALS but regularly swam out of its range, they were assigned a minimum movement range equal to the detection range of one ALS. Based on range tests, this was ca. 300 m in the study area (INBO, unpublished data). Linear regression was used to test for relationships between movement range and eel catch-release location habitat type (canal, polder ditch and pond):

$$\text{Movement range} = \alpha + \beta_1 \text{catch-release location habitat type} + \epsilon$$

A censoring problem emerged from the fact that the smallest distance measurable by the ALSs was ca. 300 m: the true value of the range distance was unknown, and so was the error between range distance and the regression line relating range distance to the catch location. Therefore, the summed squared errors cannot be minimised and ordinary least-squares methods cannot work. Therefore, censored linear regression was applied, which uses maximum-likelihood estimation (Greene, 2008). Assumptions of normality (via histo-

grams and QQ-plots) and homogeneity of variances (by plotting residuals vs. fitted values) were met after log transformation (Zuur et al., 2009, 2010).

Environmental variables determining eel movement

Environmental data

Five continuous environmental variables were linked to the departure times in the data set. These were precipitation (mm), pumping discharge ($\text{m}^3 \text{s}^{-1}$), water temperature ($^{\circ}\text{C}$), day length (min) and atmospheric pressure (hPa). Precipitation, water temperature and atmospheric pressure data were measured daily and obtained from the Flemish Environment Agency (www.waterinfo.be). Water temperature and atmospheric pressure were measured near the pumping station (coordinates: N51°16'15.8'' E3°42'43.6''), while precipitation was an average value over a large part of the study area (Fig. S2). There were two gaps of a couple of months in the water temperature data. To fill these gaps, data from a nearby canal were used (Ede canal; N51°12'15.4'' E3°26'22.3''). Both canals have a similar morphology and discharge regime and showed a high correlation (0.98) in temperature regime. A linear regression was then applied to obtain the relationship between the two data sets and fill in the gaps of the water temperature data of the studied polder area with the modified values of the nearby canal:

$$\text{water temperature LC} = 1.161941 \times \text{water temperature Ede canal} - 0.780858$$

From 1st July 2012 till 15th August 2014, pumping discharge data were

obtained daily from the Flemish Environment Agency by recordings at the pumping station. The variable "day length" was obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil/index.php>; coordinates: N51°57' E3°43'). Additionally, one categorical explanatory variable was included, namely catch-release location habitat type.

Model development

To determine the variables that significantly contributed to yellow eel movement, a generalised linear mixed model (GLMM) was applied (Mouton et al., 2011a; Verhelst et al., 2016; Zuur et al., 2009). We arbitrarily chose three movement thresholds by means of a cross-validation, and as such, three different models were constructed: an eel was considered to have moved when its swim distance was larger than 500, 1,000 or 1,500 m. For each model, the response variable "movement" was binomial: swim distances \leq a threshold value were considered as no movement, whereas higher values were considered movement. In order to give an equal weight to movement and nonmovement behaviour, bootstrapping was applied to obtain the same number of records with and without movement (Mouton et al., 2010). After the data were checked for outliers and homogeneity, a collinearity analysis was conducted (Zuur et al., 2010). As correlations were $\leq |0.70|$, all six variables were included for analysis (Dormann et al., 2013) (Table S2).

Finally, for each of the three movement thresholds, a binomial GLMM with logit link was applied to assess the effects of the explanatory variables on eel movement. In addition, the significance of three random effects in the mod-

els was tested: year, month and tag ID, the latter being a proxy for individual variability. For each full model (i.e., the model with all explanatory variables), all possible combinations with the random effects were applied, including the single random effects. The model with the lowest Akaike Information Criterion (AIC) was selected to apply a stepwise backward model selection, again based on AIC: for the 500-m threshold model, the model with the random effect "month" was selected for stepwise backward selection; for the 1,000-m and 1,500-m models, the models with both month and year as random effects were selected.

The kappa statistic (κ) was calculated to evaluate the final model; κ ranges between -1 and 1 (Goethals et al., 2007; Mouton et al., 2010). We used the "lme4" package (Bates et al., 2014) of the R environment (R Development Core Team 2017) to create the GLMMs and the "blmeco" package to check the models for overdispersion: if the scale parameter is between 0.75 and 1.4, overdispersion is considered absent. In addition, Random Forests (RF) was applied, which is a widely used machine learning technique (Breiman, 2001; Mouton et al., 2011a). The method was applied by means of cross-validation for the variables selected by the GLMM: we checked whether the variables selected by the GLMM also proved important by RF. The results of this analysis can be found in Appendix S1.

3.4 Results

3.4.1 Circadian activity patterns

Eels were most active at night with almost two times more inter-ALS movements than during daytime (Table 3.3). Moreover, 87% of the 52 tagged eels were detected at night, while only 62% were detected during daylight. The lowest activity was observed during dawn and dusk with only 40% and 17% of the eels detected during those periods respectively.

Table 3.3: Number of inter-ALS movements per circadian phase. The number of eels contributing to the number of inter-ALS movements is also given.

Circadian phase	Number of inter-ALS movements	Number of eels
Dawn	49	21
Day	377	32
Dusk	24	9
Night	744	45

3.4.2 Seasonal activity patterns

Activity patterns differed significantly between months (Welch ANOVA, $F = 18.434$, $df = 11$, $p = 2.2e-16$): the mean swim distance in summer (June–August) and autumn (September–November) was almost threefold that in winter (December–February), with the highest activity in August (Fig. 3.2a; Table S3). Activity in spring (March–May) was intermediate between winter and summer,

with activity rising from early spring towards summer.

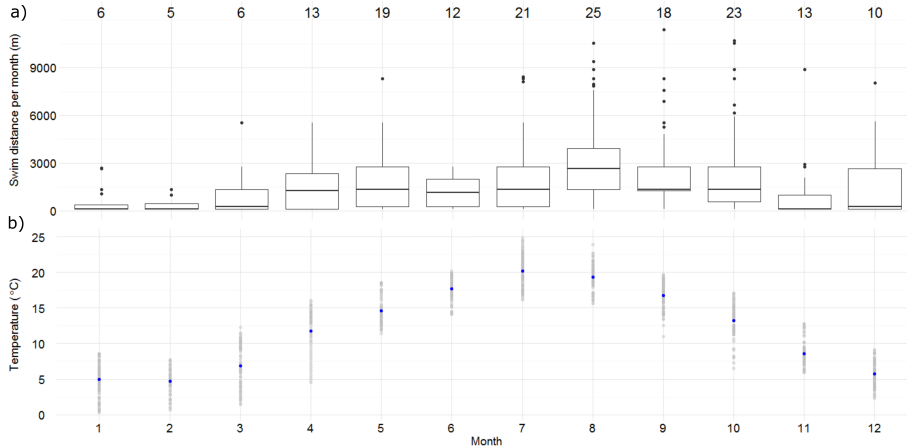


Figure 3.2: (a) Boxplot of the swim distances of all eels per month. Outliers are presented as dots above the boxplots. The number of eels taken into account is given above the different boxplots. (b) monthly water temperature (mean shown as blue dots, range by vertical lines).

Although no significant relation between water temperature and monthly swim distance was found (one-way ANOVA, $F = 0.016$, $df = 846$, $p > 0.05$), some trends were observed. When the mean water temperature rose above 10°C in April, a higher eel activity was observed compared to that in January and February (Fig. 3.2b). Activity was almost twice as high compared to March, but this was not statistically significant. Mean water temperature dropped below 10°C in November, accompanied by a significantly lower activity. Water temperature was highest during late summer, when activity peaked. However, activity was highest in August despite a lower water temperature than in July.

3.4.3 Movement range differences according to habitat type

In this study, the movement range was considered as the distance swum by an eel between the two furthest spaced ALSs during the tracking period, following the definition of Walker et al. (2014). Seven of the 52 eels were detected at only one ALS. For the latter 45 eels, the average movement range size \pm SD was 3,917.34 m \pm 4,116.64 m. No significant difference was found between eels tagged and released in different habitat types (censored regression, log-likelihood = -79.82251, df = 4, $p > 0.05$) (Fig. 3.3). Furthermore, of the 52 tagged eels, 14 (27%) were detected in another habitat than their catch habitat (Table 3.4). Notably, the eight eels caught and released in polder ditches were later found in the canal. Moreover, after release, only two returned to a polder ditch. Of the 19 eels tagged and released in ponds, three were exclusively detected in the LC, while two moved between the LC and the pond of capture. Only one eel tagged and released in the LC was detected in a pond.

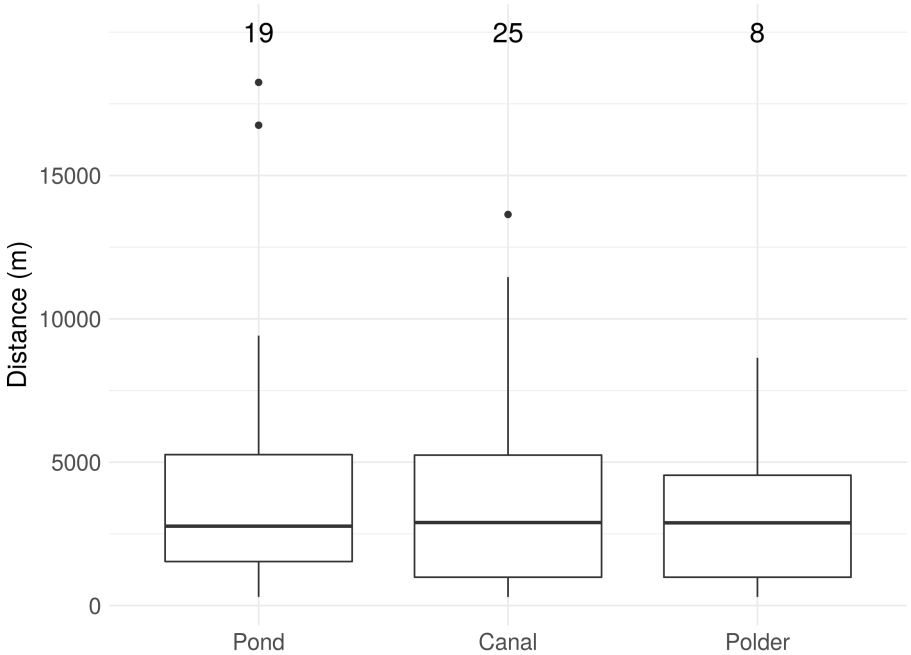


Figure 3.3: Boxplots of movement range distances (m) in the three different catch location types: ponds, canals and polder ditches. The numbers of eels caught, tagged and released at each location type are given above the different boxplots. Outliers are presented as dots above the boxplots.

Table 3.4: Number of eels detected in one or more habitat types. The catch location type gives the habitat type where the eels were caught, tagged and released. The columns "canal", "pond" and "polder ditch" give the number of eels that were detected in those habitats.

Catch location type	Detection location type		
	Canal	Pond	Polder ditch
Canal	24	0	1
Pond	5	14	0
Polder ditch	8	0	0

3.4.4 Environmental variables determining eel movement

For the model with the 500-m threshold, 45 (87%) of 52 eels were considered to have moved (801 movement records); the seven remaining eels were highly resident and stayed in the vicinity of a single ALS. The final model obtained from the backward selection only contained the variable precipitation, which had a negative relationship with eel movement (GLMM, estimated coefficient = -0.032 ± 0.014 , z value = -2.224 , $p = 0.026$; Table 3.5). When a movement threshold of 1,000 m was applied, 38 (73%) eels had moved (660 movement records). A nonsignificant negative relation with precipitation was present in the final model (GLMM, estimated coefficient = -0.034 ± 0.018 , z value = -1.914 , $p = 0.056$). The final model obtained for a movement threshold of 1,500 m (33 (63%) eels had moved, resulting in 397 movement records) showed a negative relationship with precipitation (GLMM, estimated coefficient =

-0.055 \pm 0.024, z value = -2.297, p = 0.022) and water temperature (GLMM, estimated coefficient = -0.033 \pm 0.016, z value = -2.088, p = 0.037). The impact of precipitation on eel movement was about 1.5 times that of temperature. For the results of the backward selections and Random Forests, see Table S4 and Appendix S1 respectively.

Table 3.5: Output of the three different movement threshold models (500, 1,000 and 1,500 m) after stepwise backward selection. For each model, the number of records taken into account (N) is given, as well as the Akaike Information Criterion (AIC), κ and the selected random effect with the variance and standard deviation. For the intercept and the selected variables, the estimate, standard error (SE), z value and *p* value are given.

Binomial GLMM (500 m)				
N = 1,602		AIC: 2,165 κ : 0.17		
Random effect: month (var = 0.32; SD = 0.57)				
	Estimate	SE	z-value	p-value
Intercept	-0.21	0.18	-1.13	0.259
Precipitation	-0.03	0.01	-2.22	0.026
Binomial GLMM (1,000 m)				
N = 1,320		AIC: 1,768 κ : 0.23		
Random effect:				
month (var = 0.51; SD = 0.71)				
year (var = 0.08; SD = 0.28)				
	Estimate	SE	z-value	p-value
Intercept	-0.24	0.27	-0.89	0.376
Precipitation	-0.03	0.02	-1.91	0.06
Binomial GLMM (1,500 m)				
N = 794		AIC: 1,049 κ : 0.26		
Random effect:				
month (var = 1.17; SD = 1.08)				
year (var = 0.31; SD = 0.56)				
	Estimate	SE	z-value	p-value
Intercept	0.10	0.49	0.20	0.839
Precipitation	-0.05	0.02	-2.30	0.022
Water temperature	-0.03	0.02	-2.09	0.037

3.5 Discussion

3.5.1 Circadian activity

Eels are known to be nocturnal fish which hide in crevices or bury themselves in the bottom substrate during daytime (Baras et al., 1998; McGovern and McCarthy, 1992). Our long-term (39-month) tracking study confirmed nocturnal activity: the number of inter-ALS movements was almost twice as high during the night than during daytime. Also, the majority of the eels (87%) moved at night, agreeing with findings in other tracking studies (LaBar et al., 1987; Riley et al., 2011). The daytime activity found in the present study possibly occurred mostly during overcast weather, as found by LaBar et al. (1987) and McGovern and McCarthy (1992), or during periods of increased turbidity (Baras et al., 1998). The lowest activity was found during dusk and dawn, with approximately twice the number of eels and inter-ALS movements detected during dawn compared to dusk. However, it is possible that the eels started moving during dusk or dawn, but were only detected at night due to the short duration of the twilight periods (<1 hr). Although pronounced activity during twilight was not observed in this study, it has been found for European eel (Baras et al., 1998; Riley et al., 2011), New Zealand longfinned eel (Jellyman and Sykes, 2003) and American eel (Bohun and Winn, 1966).

There are two plausible explanations for this nocturnal behaviour: foraging and predator avoidance. Eels may feed primarily at night, as their stomachs are fullest just before morning (De Nie, 1987). Eels also have a very broad diet spectrum, from invertebrates (e.g., mussels, insects, crustaceans) to fish. Many

invertebrates avoid fish predation by drifting or emerging at night (Douglas et al., 1994; Learner et al., 1990; Morgan and Waddell, 1961). Some - particularly larger - eels are piscivorous (Tesch, 2003) and may benefit from low light conditions when stalking prey (Barry et al., 2016a; Pitcher and Turner, 1986), also supporting the hypothesis that foraging at night may be more favourable. As our study only considered large eels, piscivory may have been an important strategy. Furthermore, energetic benefits could arise from a circadian rhythm, because periods of reduced activity may enable eels to meet the costs of feeding (Owen, 2001).

Predator avoidance is also often related to circadian behaviour (Ibbotson et al., 2006). Likely eel predators in our polder area include the grey heron (*Ardea cinerea* L.) and northern pike (*Esox lucius* L.), both of which are primarily active during daytime, although northern pike also feeds during twilight (Feunteun and L, 1994; Jepsen et al., 2001). In conclusion, nocturnal activity may result from both foraging behaviour and predator avoidance.

3.5.2 Seasonal activity

A trend of increasing eel activity from winter over spring to a peak at the end of summer and in autumn was found. As eels are ectothermic, a lower activity during winter was expected and is consistent with studies which found little to no activity when temperature dropped below 10°C (e.g., Riley et al. (2011); White and Knights (1997). In contrast, in a mild-climate stream in Spain, eels remained active throughout the year (Costa-Dias and Lobon-Cervia, 2008). In our study, eel activity was indeed lowest from November till March when water temperature was below 10°C. Activity rose until summer together with the

water temperature. Highest activity was found when water temperature rose above 16°C, consistent with Riley et al. (2011) and Baras et al. (1998). The latter authors stated that large yellow eels may be more active during higher water temperatures to meet increasing energetic expenditures. Nonetheless, eels were most active at the end of summer, although water temperature was lower (mean water temperature was 19.3°C in August and 16.7°C in September) than during mid-summer (mean water temperature was 20.2°C in July). This may be explained by the increasing night lengths (Béguet-Pon et al., 2015). As light negatively influences eel activity, longer nights might favour more activity as long as water temperature is above a certain threshold (Bohun and Winn, 1966). Another plausible explanation could be that the eels were more active at the end of the summer as they were seeking overwintering thermal refuge areas (Hammond and Welsh, 2009). Finally, although a distinction between yellow and silver eel behaviour was made based on the trajectory analysis of Lavielle (Lavielle, 1999, 2005), we cannot exclude that the increased activity at the end of summer was the result of eels showing movements associated with the onset of silver eel emigration.

3.5.3 Movement range

In this study, the maximum linear range between ALSs was used as a measure of movement range, as movement ranges could not be estimated in terms of area utilised (Walker et al., 2014). It should be noted that not the whole study area was covered by ALSs. Hence, reported movement ranges may be underestimated as eels could swim outside the ca. 300-m range of an ALS without being detected by an adjacent ALS. However, 15 eels (29%) were restricted to

a movement range of < 1 km, while six (12%) moved over distances in excess of 10 km. This corroborates the high interindividual variability in European eels. A range distance of maximum 285 m was found by Baras et al. (1998), while this was up to 4,150 m in a study conducted in an estuary in England (Walker et al., 2014). Baras et al. (1998) attributed the small movement range to the high complexity and numerous hiding places for eels in the studied river, leading to less foraging-related movement. The movement ranges found in our study were larger than the abovementioned studies. This could be attributed to the large size of our eels, as larger eels may have a larger movement range (Barry et al., 2016a). However, one of the six eels with a movement range > 10 km was at the growing FII stage and two were at the premigratory FIII stage. The remaining three comprised one FIV- and two FV (migratory)-staged eels. Moreover, two eels with a movement range < 1 km were FV. The large movement range of these FII- and FIII-staged eels may be attributed to silvering processes, while the small movement range of the FV-staged eels could be the result of turning back into a semiyellow stage (Svedäng and Wickström, 1997). It clearly remains difficult to define a sharp border between yellow- and silver-staged eels during long-term tracking studies.

In our study, eels were captured, tagged and released in three different habitat types. The majority of eels caught in the canal and ponds were only detected in the habitat where they were caught and released (96% and 74% respectively), demonstrating a high site fidelity.

All eels caught in large polder ditches moved to another habitat type, while none of the eels from the ponds and only one from the canal moved into a polder ditch. The lower preference for polder ditches may be explained by the

fact that these habitats were the smallest and shallowest of the system. Laffaille et al. (2003, 2004) and Lasne and Laffaille (2008) found that eels larger than 360 mm do not prefer shallow ditches with much plant cover, similar to the polder ditches in this study. As such, the results presented here illustrate that larger eels may more commonly reside in deeper habitats. This would also explain why fewer eels were caught and tagged in polder ditches (canal: $n = 25$, ponds: $n = 19$, polder ditches: $n = 8$). Moreover, electrofishing in the smallest polder ditches during the tagging period (July–August 2012) did not yield any eels. This is also why no ALSs were placed in those systems.

These results may have important implications for water management in polders. If water management aims to create eel growth habitat in polder systems or apply habitat restoration, sufficiently deep waterways should be aimed to provide habitat for large yellow eels. In addition, shallower waters with plentiful instream vegetation (e.g., reed beds) will favour the production of smaller yellow eels (Laffaille et al., 2003, 2004; Lasne and Laffaille, 2008).

3.5.4 Movement behaviour

In general, the relationships between eel movement and environmental factors based on GLMM were too weak to draw strong conclusions. We can therefore not exclude that yellow eels move largely randomly through the study area and are not influenced greatly by the environmental factors taken into account in this study. This may be confirmed by the fact that eels are opportunistic feeders (Van Liefferinge et al., 2012), and their movement may largely depend on their feeding behaviour.

3.6 Conclusion

This study describes the behaviour of large female yellow eel based on a substantial number of tagged individuals ($n = 52$), some of which have been tracked for up to 3 years (28-1,135 days). We provide evidence that European eels in freshwater polder systems are most active during the night in late summer and early autumn. We found that large female yellow eels have a high site fidelity and are not strongly affected by environmental factors (temperature, precipitation, day length, atmospheric pressure, pumping discharge). This may be attributed to the productivity of the polder system, which makes such systems highly suitable as eel growth habitats (Lasne and Laffaille, 2008; Lasne et al., 2008). In view of their high site fidelity, large female yellow eels may not encounter many human-induced connectivity problems in polder systems. Notably, upstream migration of small yellow eels (< 150 mm) does occur and is influenced by environmental variables (Feunteun et al., 2003). Hence, these animals may be influenced to a larger extent by migration barriers in polders. In addition, our study indicates that large eels prefer deeper habitats in polder systems. If measures concerning eel habitat restoration in polders are considered, areas of sufficient depth need to be maintained for large eels. A higher yellow eel survival could in turn result in a higher silver eel escapement, and as such could help meet the 40% escapement obligation imposed by the European Eel Regulation.

Chapter 4

Unimodal head-width distribution of the European eel (*Anguilla anguilla* L.) from the Zeeschelde does not support disruptive selection

Modified after:

Verhelst, P.; De Meyer, J.; Reubens, J.; Coeck, J.; Goethals, P.; Moens, T.; Mouton, A. 2018. Unimodal head-width distribution of the European eel (*Anguilla anguilla* L.) from the Zeeschelde does not support disruptive selection. *PeerJ* **6**: e5773.

For the supplemental material and appendix, we refer to the online version of the article: <https://doi.org/10.7717/peerj.5773>

4.1 Abstract

Since the early 20th century, European eels have been dichotomously classified into 'narrow' and 'broad' heads. These morphs are mainly considered the result of a differential food choice, with narrow heads feeding primarily on small/soft prey and broad heads on large/hard prey. Yet, such a classification implies that head-width variation follows a bimodal distribution, leading to the assumption of disruptive selection. We investigated the head morphology of 272 eels, caught over three consecutive years (2015 – 2017) at a single location in the Zeeschelde (Belgium). Based on our results, BIC favoured a unimodal distribution, while AIC provided equal support for a unimodal and a bimodal distribution. Notably, visualization of the distributions revealed a strong overlap between the two normal distributions under the bimodal model, likely explaining the ambiguity under AIC. Consequently, it is more likely that head-width variation followed a unimodal distribution, indicating there are no disruptive selection pressures for bimodality in the Zeeschelde. As such, eels could not be divided in two distinct head-width groups. Instead, their head widths showed a continuum of narrow to broad with a normal distribution. This pattern was consistent across all maturation stages studied here.

4.2 Introduction

Törlitz' (1922) introduction of the terms 'narrow' and 'broad' headed eels (genus *Anguilla*) led to numerous studies trying to explain these two distinct morphs (Fig. 4.1). It was even hypothesised that both morphs had different

life strategies, such as the hypothesis that broad head eels would not migrate to the sea for spawning or even be sterile (Ehrenbaum, 1930; Feddersen) or belonged to different species (Yarrell, 1831). Eels are highly flexible species with a complex life cycle. They develop as leptocephalus larvae into glass eels in the oceans, and settle as elvers in coastal and/or freshwater habitats where they grow during what is commonly known as the yellow eel stage. When eels have reached a threshold size and physiological condition, including sufficient fat reserves, they migrate back to their spawning site as silver eels (Tesch 2003).

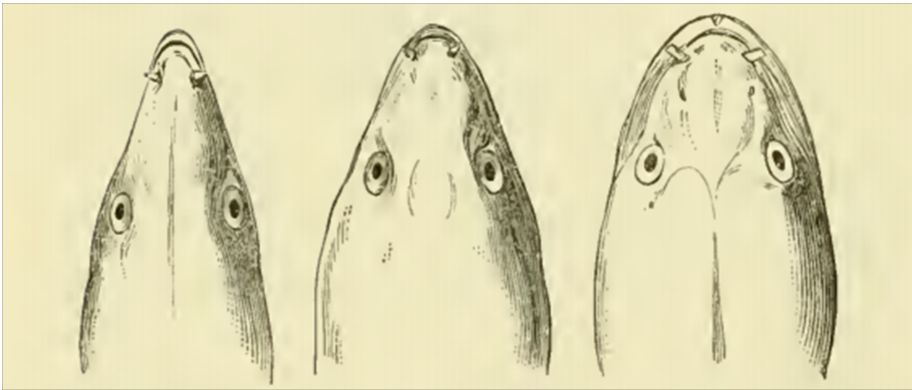


Figure 4.1: Illustration of different head width morphs with, from left to right, a narrow-headed eel, an intermediate-headed eel and a broad-headed eel (figure adopted from Benecke (1880)).

A plausible explanation for the head dimorphism is disruptive selection via resource polymorphism resulting in phenotypic plasticity, a phenomenon that occurs in many vertebrates, especially fish (Skúlason and Smith, 1995), and that essentially enables individuals of the same species to reduce intraspecific competition through resource selectivity (Schoener, 1974; Svanbäck et al.,

2008). Differences in consumed prey, for example, can lead to morphological variation in the feeding apparatus. Such a relation between feeding ecology and morphology of the feeding apparatus has been well established in animals (Iijima, 2017; Muschick et al., 2011; Saunders and Barclay, 1992). A similar relation between feeding ecology and morphology has been observed in both the European and Japanese eel. Several studies have illustrated a link between feeding strategy and head width, with narrow-headed eels feeding on small and/or soft prey (e.g. amphipods and chironomids) and broad-headed eels on large and/or hard prey (e.g. molluscs and fish) (Cucherousset et al., 2011; De Meyer et al., 2016; Ehrenbaum, 1930; Kaifu et al., 2013; Lammens and Visser, 1989; Provan and Reynolds, 2000). The broader heads thus reflect better developed jaw closing muscles and a relatively broader skull, features which facilitate the consumption of hard and/or large prey items (De Meyer et al., 2016).

Yet, the European eel is an opportunistic animal (Lammens et al., 1985; Schulze et al., 2004; Van Liefferinge et al., 2012), though specialization on specific prey items has been observed (Barak and Mason, 1992), challenging the dichotomous and strongly deterministic characterization into 'broad' and 'narrow' heads based on feeding behaviour. Indeed, head dimorphism may not be entirely attributed to differences in foraging. For instance, narrow headed Japanese eels grow faster than broad heads (Kaifu et al., 2013) and genetic support for this hypothesis has recently been found in European eel (De Meyer et al., 2017b). Moreover, certain genes involved in growth speed, such as *growth hormone-1*, are also involved in salinity preference (Iwata et al., 1990); thus, eels preferring freshwater grow more slowly than eels favouring marine waters (Edeline et al., 2005). Hence, the basis for head dimorphism in eels may

be much more complex than originally thought. Despite substantial research related to eel head widths, many knowledge gaps remain. For instance, head width of glass eels follows a unimodal distribution (De Meyer et al., 2015). Consequently, a strict dichotomous division of such glass eels into a narrow and a broad headed morph is impossible, as a gradual transition exists from narrower to broader headed eels with many intermediate forms. Still, many studies have dichotomously classified narrow and broad headed eels using a ratio-based threshold: eels with a head width over total body length ratio smaller than 0.033 are considered narrow heads, while eels with larger ratios are broad heads (Barry et al., 2016a; Kaifu et al., 2013; Lammens and Visser, 1989; Provan and Reynolds, 2000). However, head width increases allometrically with total length (De Meyer et al., 2015, 2017a; Lammens and Visser, 1989), so larger eels may be wrongly classified as broad heads.

In contrast to the above-mentioned unimodal head-width distribution in glass eels, the head width of yellow eels has been suggested to follow a bimodal distribution (Ide et al., 2011; Kaifu et al., 2013). Bimodality would occur during the maturation stage after glass eel settlement. Six different maturation stages have been identified from the yellow eel stage onwards (Durif et al., 2005): a sexually undifferentiated yellow stage (I), a female yellow stage (FII), a female intermediate stage (FIII), two female silver eel stages (FIV and FV) and a male silver eel stage (MII). It is therefore possible that the unimodality found in glass eels shifts to bimodality during further development through these stages.

From an evolutionary point of view, variations in head shape may arise from different selective pressures at many locations, or even disruptive pressures such as observed on a side channel of the Frome River (Cucherousset

et al., 2011): individuals with intermediate traits would have a lesser fitness than individuals with more extreme traits, because they may be less efficient in the consumption of both soft/small prey and hard/large prey in comparison to the more extreme morphs (Martin and Pfennig, 2009). Head morphology may also affect an eel's fitness in yet another way: narrow-headed eels have a more hydrodynamic body shape and may therefore migrate faster or in a more energetically favourable way than broad heads (De Meyer et al., 2016; Van Wassenbergh et al., 2015), increasing their chances of successful spawning.

Despite the substantial research related to head dimorphism and studies finding evidence for bimodality, in this study, we propose the conservative null hypothesis that eels from a single river drainage do not show disruptive selection related to eel head width by assessing four sub-hypotheses: (1) Head-width variation follows a unimodal distribution, and (2) this distribution does not differ between different maturation stages; (3) body condition does not differ according to head width, and (4) eels with a narrower head width migrate at a similar speed as eels with a broader head width.

4.3 Methods

4.3.1 Study area

The River Schelde is approximately 360 km long and has a drainage area of 21,863 km² (Fig. 4.2). The river originates on the plateau of Saint-Quentin in France and runs through Belgium into the North Sea in The Netherlands. The Schelde is one of the few European rivers with a well-developed estuary. It is

approximately 160 km long and has a complete salinity gradient from marine to a tidal freshwater zone, including extensive freshwater, brackish and salt marshes. The Belgian part of the Schelde Estuary (i.e. the Zeeschelde) runs from Gent to Antwerp. It is well-mixed and characterized by strong currents, high turbidity and a large tidal amplitude up to 6 m (Seys et al., 1999). It has a length of 105 km, a width of 50 m to 1350 m, and an average discharge of $100 \text{ m}^3 \text{ s}^{-1}$. In addition, several tributaries discharge into the Zeeschelde. Our study area only comprised the Zeeschelde. There is no commercial fishing in this area and fyke fishing is prohibited in Belgium since 2009, yet, recreational fishing for eels does occur.

4.3.2 Data collection

Over three consecutive years (i.e. 2015 till 2017), 272 eels were caught in summer and autumn with double fyke nets (mesh size = 8 mm) downstream the tidal weir (Merelbeke) in the freshwater part of the Zeeschelde. The dorsal view of the head was photographed with a digital camera on graph paper and several morphometric features were measured in order to determine the eel maturation stages according to Durif et al. (2005): total length (TL, to the nearest mm), body weight (W, to the nearest g), the left vertical and horizontal eye diameter (ED_v and ED_h respectively, to the nearest 0.01 mm) and the length of the left pectoral fin (FL, to the nearest 0.01 mm) (Table 4.1). Eels of all six different maturation stages were caught: sexually undifferentiated yellow eels (I, $n = 51$), female yellow eels (FII, $n = 68$), premigrant female eels (FIII, $n = 91$), two female silver eel stages (FIV and FV, $n = 15$ and $n = 40$, respectively) and the male silver eel stage (MII, $n = 7$).

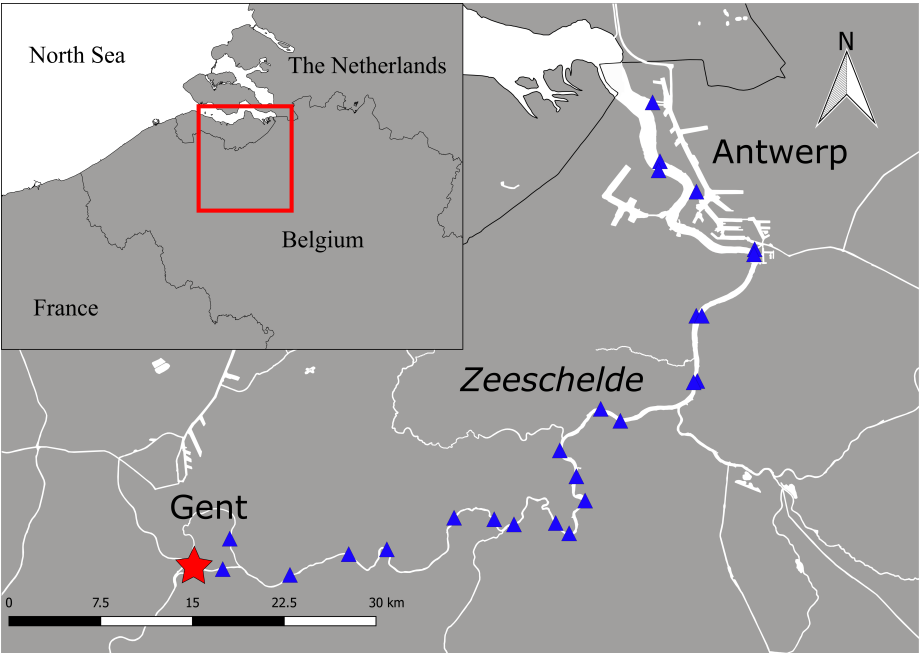


Figure 4.2: Study area with the catch location at the tidal weir in Merelbeke (asterisk) and the position of the acoustic listening stations (triangles) in the Zeeschelde.

Table 4.1: Numbers of eels caught per maturation stage with the different morphometrics: total length (TL), body weight (BW), left horizontal and vertical eye diameters (ED_h and ED_v , respectively) and left pectoral fin length (FL). Means \pm SD (range) are given.

Stage	Number	TL (mm)	BW (g)	ED_h (mm)	ED_v (mm)	FL (mm)
I	51	345 ± 76 (184 - 501)	76 ± 46 (9 - 222)	4.11 ± 0.97 (2.01 - 576)	3.84 ± 0.92 (1.67-5.39)	15.42 ± 3.78 (7.88-25.44)
FII	68	499 ± 47 (426-642)	213 ± 76 (88-478)	5.93 ± 0.48 (4.66-7.02)	5.51 ± 0.46 (4.59-6.65)	23.22 ± 2.50 (16.68-29.98)
FIII	91	639 ± 78 (505-835)	504 ± 199 (141-1106)	7.65 ± 0.70 (6.28-9.08)	7.14 ± 0.69 (5.46-9.70)	30.38 ± 3.78 (24.24-40.32)
FIV	15	815 ± 67 (707-932)	1173 ± 248 (771-1830)	10.43 ± 0.81 (9.31-12.49)	9.76 ± 0.79 (8.91-11.86)	41.17 ± 4.54 (30.84-48.18)
FV	40	630 ± 70 (510-775)	502 ± 177 (189-912)	8.86 ± 0.94 (7.40-11.18)	8.40 ± 0.90 (6.95-10.39)	32.80 ± 4.03 (25.84-45.37)
MII	7	386 ± 3 (335-428)	111 ± 39 (66-170)	6.69 ± 1.26 (4.47-8.16)	6.22 ± 1.09 (4.27-7.52)	20.06 ± 3.89 (12.97-25.75)

4.3.3 Data analysis

Head width distribution

ImageJ (Abràmoff et al., 2004) was used to measure head width (HW) on the photographs as two times the snout length, which is defined as the distance from the midpoint between the anterior end of the eyes to the tip of the snout (Fig. 4.3). This way, HW was measured at the postorbital region where the jaw muscles can be found, an important region related to broad- and narrow-headedness (De Meyer et al., 2016). In addition, head length (HL) was measured as the distance from the tip of the snout to the start of the pectoral fins and consequently, HW/HL was calculated for each eel. Since HW/HL tends to increase slightly with TL, the unstandardized residuals were first calculated via linear regression between HW/HL and TL (see Appendix for more details). Subsequently, the residual values were used for a mixture analysis in the R environment (R Development Core Team 2017). To analyze whether the head shape variation followed a unimodal or bimodal distribution, two different penalized model selection criteria were calculated: the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC). Both model selection criteria are commonly applied with lower values indicating better models, but have different qualities and merits (Aho et al., 2014). Essentially, AIC is applied when the analysis is exploratory and strives for efficiency, that is, the method maximizes predictive accuracy. Consequently, AIC tends to select the most complex model as the true model (Kass and Raftery, 1995). BIC on the other hand is used for confirmatory analysis and strives for consistency (Aho et al., 2014). Related to unimodal and bimodal distribution selection, according

to Brewer (2003), a unimodal distribution is strongly and moderately supported when $\Delta AIC < -8$ and < -5 , respectively. If ΔAIC ranges from $-5 - 5$, there is equal support for both a unimodal and bimodal distribution, while values > 5 and > 8 moderately and strongly support bimodality, respectively. We used the 'mclust' package of the R environment for model selection criterion calculation, and the 'mixtools' package for visualizations (R Development Core Team 2017).

Maturation stages and sex

First, we checked if the unimodal distribution held true for the different maturation stages (I, FII, FIII, FIV, FV and MII) separately. Since the assumptions of normality (histograms and QQ-plots) and homogeneity of variance (plotting residuals vs. fitted values) were met (Zuur et al., 2010), a one-way ANOVA was conducted on the residual variance of each maturation stage. Next, the AIC and BIC were calculated for each maturation stage as mentioned above.

Body condition

To analyse if body condition changes according to HW, the relative condition factor (Kn) (Le Cren, 1951) was used. Kn takes allometric growth into account; when < 1 , fish are in a worse condition than expected, while > 1 indicates a better condition:

$$Kn = W/aL^b$$

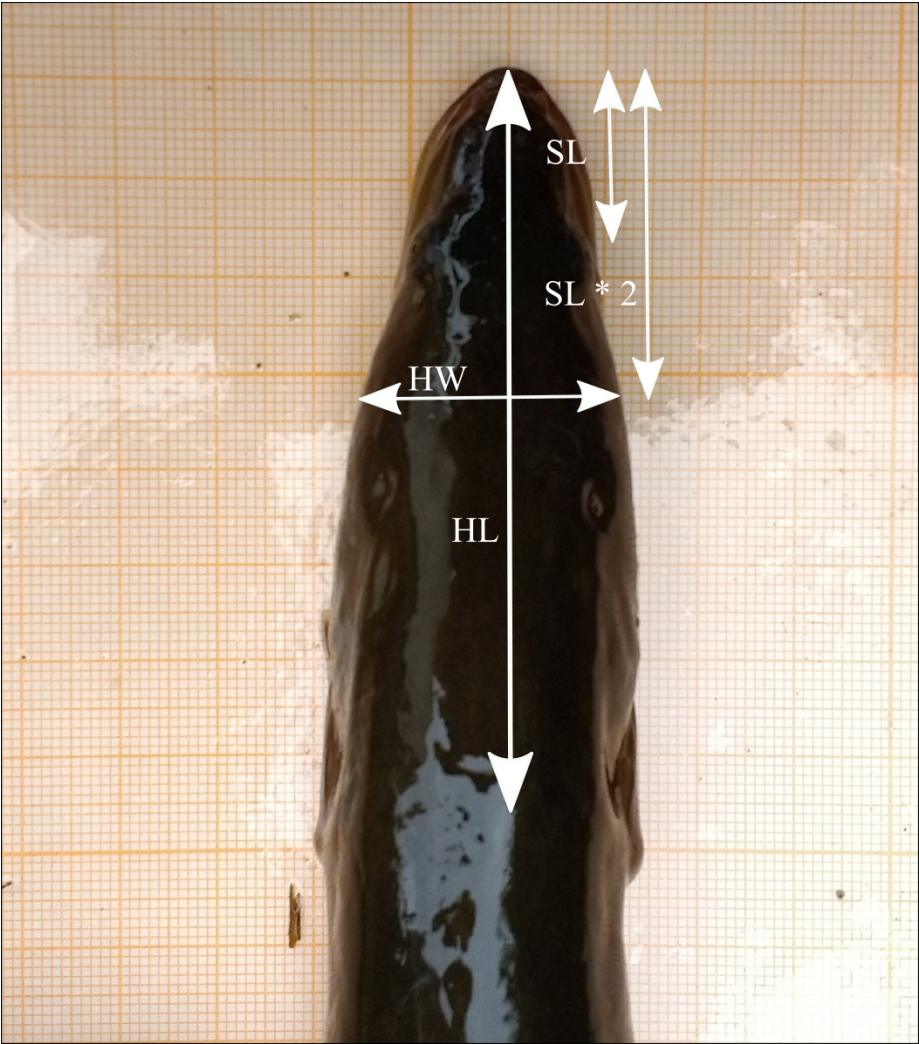


Figure 4.3: Head measurements based on the dorsal picture of an eel's head on graph paper (HL: head length, HW: head width, SL: snout length).

where a is a constant and b an exponent varying from 2.5 to 4 (Hile, 1936; Martin, 1948): $b = 3$ indicates isometric growth and $b \neq 3$ allometric growth ($b < 3$ for fish becoming more fusiform as they grow and $b > 3$ for fish becoming progressively less slender). In the formula, total length (L) and body weight (W) have a logarithmic relationship:

$$\log(W) = \log(a) + b\log(L)$$

where b is the slope of the line and $\log a$ the intercept (Le Cren, 1951). To test if K_n changes according to HW, linear regression was applied (data followed a normal distribution and the variances were homogenous). A power analysis was conducted with the pwr R package to detect an effect of a given sample size under the 5 % significance level.

Migration speed

To determine migration speeds, 51 migrating eels were tagged with coded acoustic transmitters (V13, 13 x 36 mm, weight in air 11 g, frequency 69 kHz, estimated battery life: 1021 – 1219 days (battery lifetime depended on specific transmitter settings)) from VEMCO Ltd (Canada) and tracked in the Zeeschelde by an acoustic network of 25 ALSs (VR2W, VEMCO Ltd) (approval by the Ethical Committee of the Research Institute for Nature and Forest (ECINBO09)). After anaesthetizing the eels with 0.3 ml·L⁻¹ clove oil, tags were implanted according to Thorstad et al. (2013) with permanent monofilament. Eels recovered in a quarantine reservoir for approximately one hour and were subsequently released at the ALS closest to their catch location. Data were pro-

cessed as previously described in Verhelst et al. (2018a). The residency times (i.e. the time between arrival and departure at an ALS) were calculated, which allowed us to reduce the data by accumulating the number of detections during a fixed period of time. We applied an absence threshold of one hour (i.e. the maximum time permitted between detections within a single residency period) and a detection threshold of one detection (i.e. the minimum number of detections required for a residency period). As such, the residency search resulted in intervals with arrival and departure times per eel at each ALS.

Not all eels migrated upon tagging. Therefore, an eel was considered migratory when it travelled net ≥ 20 km downstream during ≤ 40 days (Verhelst et al., 2018b). Within that period, we selected the records from the most upstream station down to the most downstream station (i.e. sometimes an eel aborted its migration and moved back upstream). The 20-km threshold is based on the maximum range distance found for yellow eels (i.e. 18 km) (Verhelst et al., 2018c) plus two times the one km detection range of an ALS in the SE (i.e. the spatial error for the migration range). The 40-days threshold is based on the finding that eels not migrating net ≥ 20 km downstream during that period, arrested their migration to proceed in a next season. For two eels, applying the above assumptions resulted in the selection of two migration phases per eel: they arrested their migration, subsequently moved back upstream near their catch location, and eventually resumed migration two and twelve months later. For those two eels, we only used the second migration phase for analysis. Next, we calculated the migration speed as the time needed to cross the distance between the detections at the two most distant ALSs in the migration phase. To analyse if the migration speed differed according to HW, a linear mixed effects model (transmitter ID as a random effect to account for

autocorrelation) was applied. We also applied the linear mixed effects model after removal of three extreme values. The nlme R package was used to conduct the linear mixed effects model (R Development Core Team 2017). A power analysis was conducted with the pwr R package to detect an effect of a given sample size under the 5 % significance level.

4.4 Results

4.4.1 Head-width distribution

The linear regression of the HW/HL ratio to TL proved significant ($F(1, 270) = 51.26$, $p = 7.66e-12$ with R^2 (adjusted) = 0.16), and revealed the following relationship (Fig. 4.4):

$$HW/HL = 0.26244 + 0.00087 * TL$$

The data followed a normal distribution (Shapiro-Wilk test, $W = 0.99$, $p > 0.05$), yet showed slightly right-tailed skewness. BIC proved lowest for the unimodal distribution, favoring that distribution. AIC on the other hand was lowest under the bimodal distribution, but differences between unimodality and bimodality were consistently small (Table 4.2). Moreover, when using the criteria of Brewer (2003), our data provided equal support for both unimodality and bimodality under AIC, since ΔAIC ranged between -5 and +5. However, visualization of the bimodal distribution indicated a strong overlap between the two normal distributions (i.e. one normal distribution is almost completely encompassed by the other) (Fig. 4.5). Based on these results, we

concluded that a unimodal distribution best fitted our data.

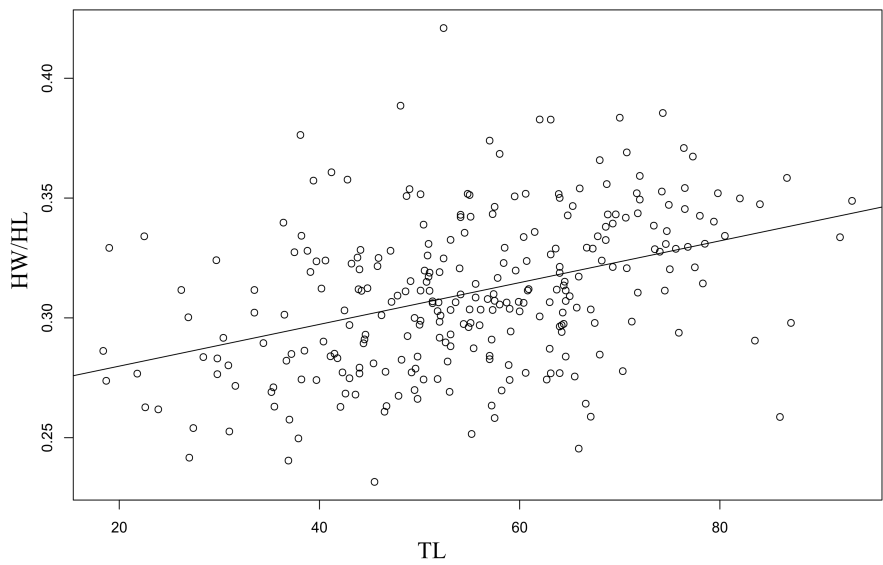


Figure 4.4: Regression between the ratio head width : head length (HW/HL) and total body length (TL).

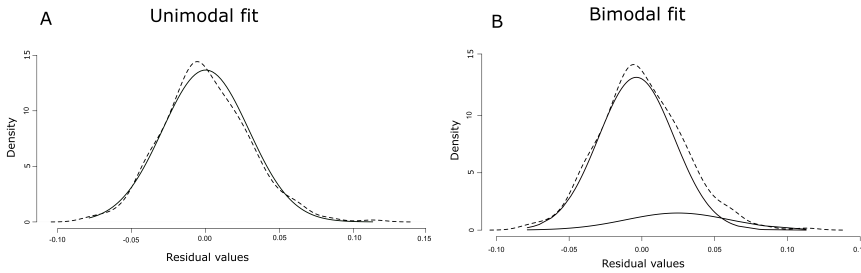


Figure 4.5: Unimodal (A) and bimodal fit (B) of normal distributions (solid lines) on the density distribution of the residuals (dashed lines).

Table 4.2: Values of the model selection criteria AIC and BIC for a unimodal and bimodal distribution.

Model selection criterion	Unimodal	Bimodal
AIC	-1148	-1149
BIC	-1141	-1134

4.4.2 Maturation stages and sex

We did not find a significant difference in residual variation between the different maturation stages (one-way ANOVA, $F = 0.83$, $DF = 5$, $p > 0.05$), although the variation for MII eels, which was based on only seven individuals, was slightly higher than for the other groups (Fig. 4.6). Similar to the total dataset and following the guidelines of Brewer (2003), BIC favored the unimodal

distribution for all stages except FII and MII, while uni- and bimodality were equally supported by AIC between eel stages (Table 4.3). Yet again, there was a strong overlap between the two normal distributions under the bimodal model (Fig. 4.7). Notably, due to the low number of observations, especially for FIV- and MII-eels, more data is needed to draw strong conclusions on the life stages.

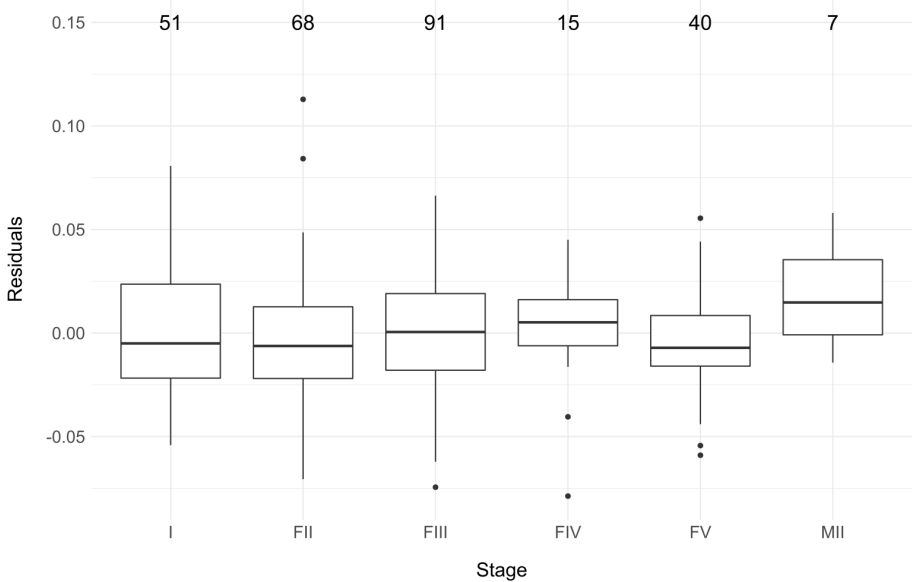


Figure 4.6: The residual variation according to the six maturation stages (I,FII, FIII, FIV, FV and MII). The number of eels per stage are indicated above the boxplot.

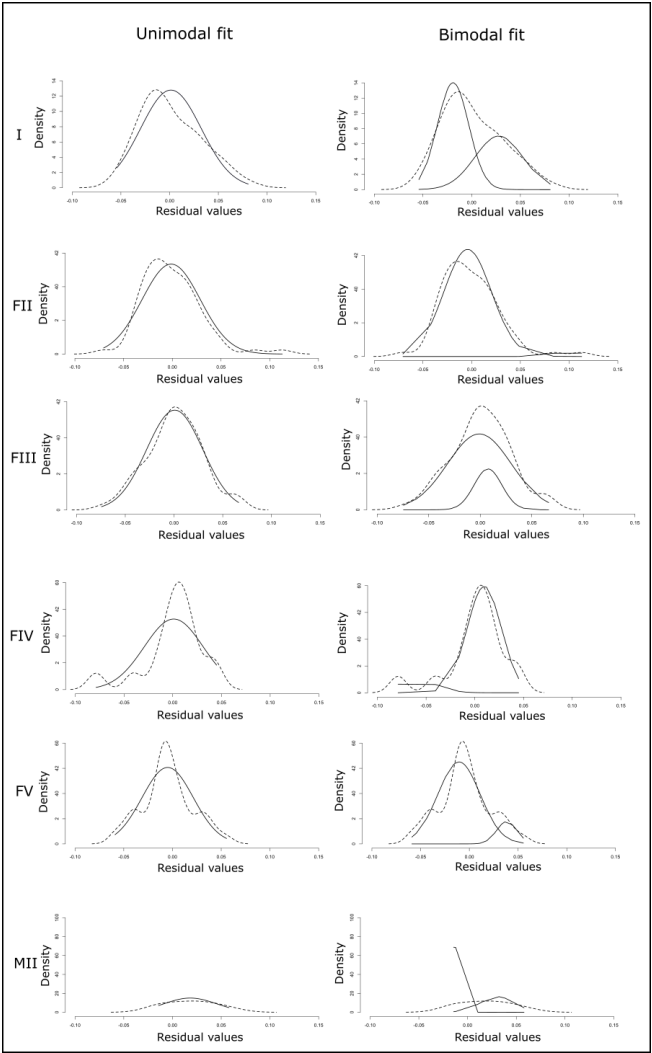


Figure 4.7: Unimodal and bimodal fit of normal distributions (solid lines) on the density distribution of the residuals (dashed lines) for each maturation stage (I, FII, FIII, FIV, FV and MII).

Table 4.3: The AIC and BIC per maturation stage (I, FII, FIII, FIV, FV and MII) for both unimodal and bimodal support.

Stage	Unimodal		Bimodal	
	AIC	BIC	AIC	BIC
I	-206	-202	-208	-200
FII	-282	-277	-288	-279
FIII	-384	-379	-380	-370
FIV	-59	-58	-60	-57
FV	-175	-171	-171	-164
MI	-28	-28	-30	-30

4.4.3 Body condition

Values for the constants a and b of the logarithmic relationship between weight and total length were a = 0.00068 and b = 3.24,

$$Kn = W/0.00068L^{3.24}$$

indicating that eels become plumpier as they grow ($b > 3$). Kn was on average 1.01 ± 0.15 (range: 0.51 – 1.61) and increased significantly with a broader HW (linear regression, $F(1, 270) = 6.30$, $p = 0.01$ with R^2 (adjusted) = 0.02) (power =

1.00) (Fig. 4.8):

$$Kn \sim 1.01 + 0.80 * \text{unstandardizedresiduals}$$

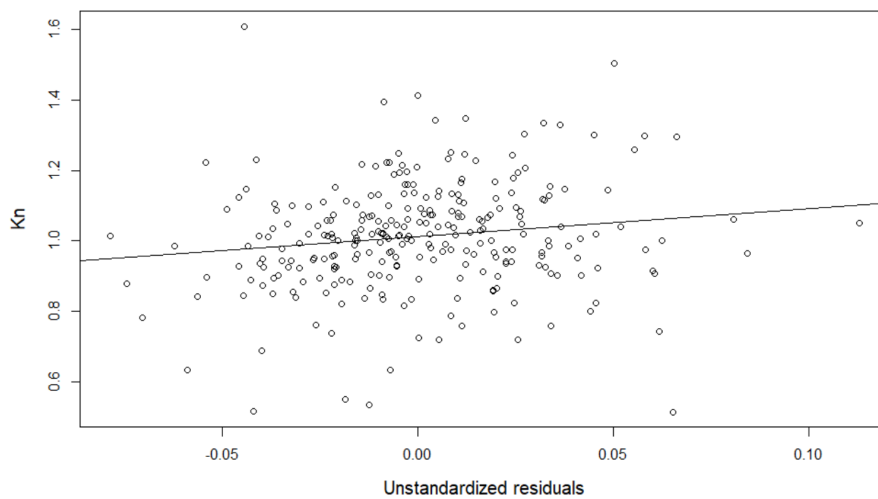


Figure 4.8: The relative condition (Kn) increases with a broader head width (unstandardized residuals).

4.4.4 Migration speed

Migration speed was on average $0.05 \pm 0.08 \text{ m s}^{-1}$ (range: $0.01 - 0.40 \text{ m s}^{-1}$) and did not change significantly according to HW (linear mixed effects model, t-value 0.63, $DF = 49$, $p = 0.53$; Fig. 4.9), not even after removal of the three outliers (linear mixed effects model, t-value 1.14, $DF = 46$, $p = 0.26$) (power =

0.77).

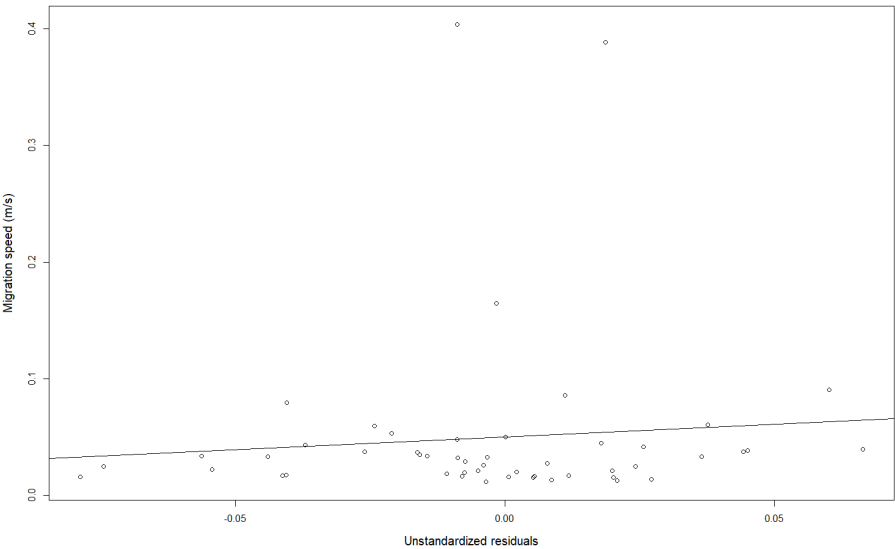


Figure 4.9: Migration speeds in relation to the head width (unstandardized residuals).

4.5 Discussion

4.5.1 Head-width distribution

Despite the dichotomous characterization of eel HW in previous research based on eels from multiple locations and/or habitats (Ide et al., 2011; Pro-man and Reynolds, 2000), our study at a single location in the Zeeschelde does not support clear bimodality and hence also does not provide any in-

dication for disruptive selection. Instead, BIC indicated unimodality and AIC provided equal support for a unimodal and a bimodal distribution (Brewer, 2003). Nonetheless, AIC tends to select the more complex model over the true model (Kass and Raftery, 1995). Indeed, the equal support for both unimodality and bimodality is likely caused by the strong overlap between the two normal distributions in the bimodal model, with one normal distribution being almost completely encompassed by the other. Such overlap can hamper the distinction between a unimodal and a bimodal distribution (Hendry et al., 2006). Due to this strong overlap, we conclude that eels in the present study cannot be strictly classified into narrow- and broad-headed individuals based on a single threshold (Barry et al., 2016a; Ide et al., 2011; Lammens and Visser, 1989; Provan and Reynolds, 2000). Instead, a unimodal distribution indicates that eels have narrower or broader heads towards the extremes of a continuous normal distribution with many intermediate morphs. Notably, the slight right-skewness in the HW variation in the present study may be attributed to other selective pressures than disruptive selection. For instance, these data could be interpreted as an indication for a unidirectional pressure towards larger head widths, perhaps reflecting selection for predation on larger or hard-bodied prey. As such, skewness in one direction or the other may vary widely between locations and habitats. Although the number of eels in our study was relatively limited ($n = 272$), analysis of 50%, 75% and 90% of the data yielded very similar results (Fig. S1, Table S1). Moreover, the overlap between the two normal distributions under the bimodal fit tended to increase with the percentage of data taken into account (i.e. 50% to 90%), indicating a stronger support for unimodality as more data was taken into account. In addition, other studies have used similar or even lower numbers (Barry et al., 2016a; Cucherousset

et al., 2011; Kaifu et al., 2013; Proman and Reynolds, 2000).

(Ide et al., 2011) did find evidence of bimodality and observed that head shape variation in European eel in Belgium was best described by two unimodal distributions with overlapping tails. This discrepancy may be explained by the fact that these authors covered different sampling locations, often characterized by different feeding conditions. If head shape depends on prey type, then eels caught at locations with a higher abundance of soft-bodied/small prey will tend to the narrow side of the HW distribution, while the opposite will hold true for locations dominated by hard-bodied/large prey. When eels of two such contrasting locations are pooled together, a bimodal distribution would be more likely to occur.

Under the assumption that HW distribution is mainly the result of food choice (Lammens and Visser, 1989; Proman and Reynolds, 2000), the observed unimodal distribution in the Zeeschelde could be explained by an opportunistic behaviour of eels (Lammens et al., 1985; Schulze et al., 2004; Van Lieferinge et al., 2012). Feeding on a wide range of prey items reduces selective pressures towards head shapes that are more specialized for the consumption of either hard or soft prey. Predatory fish of cold-temperate waters tend to be opportunistic feeders, as productivity in these areas is often relatively low and prey abundance depends on season and temperature (Keast, 1979), implying that the most available prey has the highest chance of being consumed. However, eels can also display a remarkable preference for specific prey items, irrespective of their availability (Barak and Mason, 1992).

Other factors than food could also explain the occurrence of head dimorphism: narrow headed eels have been suggested to be more crepuscular and for-

age in the littoral zone, while broad headed eels would be more active at night and in the limnetic zone (Barry et al., 2016a; Cucherousset et al., 2011). In addition, bimodality may be present mostly in areas where eel densities are high, leading to intraspecific competition through resource polymorphism and consequently to different head shapes (e.g. in lakes with artificially stocked eels) (Lammens and Visser, 1989).

4.5.2 Maturation stages, sex and body condition

Eel maturation stages are commonly classified according to Durif et al. (2005) (Barry et al., 2016a; Bultel et al., 2014; Stein et al., 2015). Although the method may not be 100% conclusive, distinction between male and female silver eels was confirmed in our study as males showed the typical silvering characteristics (visible lateral line, large, melanised pectoral fins, dark dorsal side, silver-white ventral side and large eyes) and had a TL < 45 cm (Tesch, 2003).

De Meyer et al. (2015) hypothesized that the absence of a clear bimodal pattern in glass eels, contrasting with its presence in yellow eels (Ide et al., 2011), may be attributed to a trophic niche segregation between different eel developmental stages. However, we found no bimodal pattern in the Zeeschelde in any of the maturation stages defined by Durif et al. (2005). Like for the total dataset, BIC favored a unimodal distribution and AIC provided equal support for a unimodal and a bimodal distribution. Again, the latter likely results from the strong overlap between two normal distributions. Given the small number of specimens in the present study, especially in FIV (15) and MII (7) eels, we can, however, not rule out the possibility that the distribution could be skewed due to the tail of the distribution (Hendry et al., 2006). The absence of a clear

bimodal distribution could again be explained by the opportunistic behavior of the eels (Lammens and Visser, 1989; Schulze et al., 2004; Van Liefferinge et al., 2012). Specifically, since our study included eels from a single location only, opportunistic feeding and low to moderate population density would render disruptive selection pressure towards feeding specificity unlikely during the different maturation stages in the Zeeschelde.

Counter to Cucherousset et al. (2011), who argued that the better body condition of both narrow and broad headed eels compared to intermediate headed eels was the result of disruptive selection (Martin and Pfennig, 2009; Skúlason and Smith, 1995), body condition of eels in the Zeeschelde also did not support the idea of disruptive selection, since body condition increased along with HW, suggesting unidirectional selection. However, the small amount of variation explained by the model suggests that factors other than head width play a more prominent role in body condition variation.

4.5.3 Migration speed

Combining telemetry with HW classification, Barry et al. (2016a) observed a larger home range for broad headed yellow eels. In addition, circadian activity patterns differed, with narrow-headed yellow eels being more crepuscular while broad-headed yellow eels more nocturnal. Here, we preliminarily analysed if the downstream migration speed (i.e. movement at meso-scale) of silver eels in the Zeeschelde differed according to HW. Migration speed is often calculated to make predictions about progression (Aarestrup et al., 2010; Breukelaar et al., 2009; Bultel et al., 2014), swimming performance (Russon et al., 2010; Van Den Thillart et al., 2004; van Ginneken et al., 2005) or the chances

of reaching the spawning area in time (Righton et al., 2016). Our results suggest that at least the progression of silver eels is not influenced by their head morphology. Nonetheless, swimming experiments in swim tunnels may shed more light on the relationship between HW and different aspects of migration and swimming performance (van Ginneken et al., 2005).

4.6 Conclusion

In contrast to evidence for a bimodal head-width distribution of European eel (Ide et al., 2011), we found support for a unimodal distribution in European eel HW variation at a location in the Zeeschelde, both when separately analyzing different maturation stages and when looking at the total dataset. This indicates a lack of evidence for disruptive selection but does not exclude unidirectional pressures on variation in eel head shapes. Finally, downstream migration speed of silver eel at a meso-scale was not influenced by HW morphology. We conclude that eels in the Zeeschelde could not be dichotomously classified into narrow and broad heads, but rather represent a continuum of specimens with narrow to broad heads following a normal distribution.

Chapter 5

Selective tidal stream transport in silver European eel (*Anguilla anguilla* L.) – Migration behaviour in a dynamic estuary

Published as:

Verhelst, P.; Bruneel, S.; Reubens, J.; Coeck, J.; Goethals, P.; Oldoni, D.; Moens, T.; Mouton, A. 2018. Selective tidal stream transport in silver European eel (*Anguilla anguilla* L.) - Migration behaviour in a dynamic estuary. *Estuarine, Coastal and Shelf Science* **213**: 260 - 268.

For the supplemental material and appendix, we refer to the online version of the article: <https://doi.org/10.1016/j.ecss.2018.08.025>

5.1 Abstract

Different fish species use selective tidal stream transport (STST) to efficiently migrate through strong tidal systems to complete their life cycle, but the use of STST by silver European eels is still controversial. In this study, we found strong evidence that silver European eels apply STST. The results illustrate that eels can distinguish between ebb and flood and suggest that tides play a role in orientation, either directly or indirectly. The general migration speed was higher in the downstream part of the estuary compared to the upstream part, while tidal migration speed was equal in both parts, indicating that eels migrated more consistently in the downstream part. The results of this study give insight in how a diadromous species migrates through an estuary and underline the importance of the tides.

5.2 Introduction

Animal migration is a persistent and unidirectional movement, characterized by the temporary inhibition of station keeping responses such as foraging, territorial behaviour and commuting (Kennedy, 1985). In the animal kingdom, many groups rely on successful migration to complete their life cycle (e.g. arthropods, fish, birds, mammals...), each with different goals such as reproduction or reaching a more qualitative habitat (Berger, 2004; Dingle, 2006; Stern, 2009; Weitkamp and Neely, 2002). Many fish species, for instance, migrate between freshwater and marine environments for spawning (i.e. diadromy) (e.g. Acipenseridae, Alosinae, Anguillidae, Salmonidae). Con-

sequently, diadromous fish have to overcome substantial distances which come with a high energetic cost. Due to the high energetic cost of migration and the low adult survival, some of these species have developed semelparity (Crespi and Teo, 2002). Consequently, a bioenergetic trade-off between migration and reproduction may exist for semelparous fish species, especially since many will stop feeding during migration (Bernatchez and Dodson, 1987): the smaller the energy expenditure during migration, the larger the amount of energy that may remain available for gonad maturation (Glebe and Leggett, 1981; Jonsson et al., 1991; Marshall et al., 1999).

An example where migration can have important bioenergetic repercussions is migration through strong tidal systems. To reduce energy loss in such systems, fish may perform selective tidal stream transport (STST): an animal ascends into the water column with the appropriate tide and rests on or in the bottom during the opposite tide (Walker et al., 1978). STST has been observed for different marine fish species, such as cod (*Gadus morhua* L.) (Arnold et al., 1994), sole (*Solea solea* L.) (Walker et al., 1980) and plaice (*Pleuronectes platessa* L.) (Metcalf et al., 1990; Walker et al., 1978), but also for diadromous fish species in estuaries such as sockeye salmon (*Oncorhynchus nerka* Walbaum) (Levy and Cadenhead, 1995) and flounder (*Platichthys flesus* L.) (Jager, 1999). Yet, the behaviour is not universal: Silva et al. (2017) did not observe STST for upstream migrating river lamprey (*Lampetra fluviatilis* L.) in an English estuary.

A fish species of particular interest to study STST is the European eel. Since it is semelparous and does not feed during migration, it must rely on its accumulated fat reserve for successful spawning (Tesch, 2003). In rivers and polders, for example, silver eels migrate during peak discharges (Piper et al.,

2015; Travade et al., 2010; Verhelst et al., 2018c; Vøllestad et al., 1986). Migration during peak discharges might help silver eels to conserve energy by reducing swimming activity and shorten the period required to reach the sea (Trancart et al., 2018). In estuaries, however, current direction changes twice a day following a sinusoidal pattern (i.e. the tide). In those systems, it would be energetically beneficial to use STST during migration.

STST has been observed in the glass eel stage (i.e. the young recruits reaching coastal waters and entering freshwater systems) of different eel species (European eel (Beaulaton and Castelnaud, 2005; Creutzberg, 1961; Trancart et al., 2012), American eel (*A. rostrata*) (Sheldon and McCleave, 1985), shortfin eel (*A. australis*) (Jellyman, 1979), New Zealand longfin eel (*A. dieffenbachii*) (Jellyman, 1979), Japanese eel (Dou and Tsukamoto, 2003), Celebes longfin eel (*A. celebesensis*) (Sugeha et al., 2001), Giant mottled eel (*A. marmorata*) (Sugeha et al., 2001) and Indian shortfin eel (*A. bicolor pacifica*) (Sugeha et al., 2001)). Due to their small size and accompanying weak swimming strength, it is unlikely that glass eels can migrate against the strong tidal forces and river currents for extended periods of time Adam et al. (2008); hence, STST allows them to migrate upstream. In addition, STST has been found in the silver eel stage of both American (Barbin et al., 1998; Béguer-Pon et al., 2014; Parker and McCleave, 1997) and European eels (McCleave and Arnold, 1999). However, for the latter, conclusions were based on only two individuals, which were translocated from freshwater to the marine environment and then tracked for a very short time (max 58 h) and net distance (max 72.2 km). Yet, both Barry et al. (2016b) and Huisman et al. (2016) observed that the majority of their tracked silver eels migrated during ebbing tide in an estuary and in the North Sea, respectively. In contrast, tracking studies by Tesch (1992) and Bultel et al. (2014) found no

relationship with the tides, illustrating ambiguity regarding the use of STST in European eels.

We challenge the hypothesis that European silver eels use STST in a highly dynamic estuary and addressed two research questions: 1) Do migratory eels apply STST, and 2) at what speed do they migrate through the estuary? This study provides insight in silver eel migration behaviour in a highly dynamic ecosystem and may support management measures for estuary restoration and tidal barrier passage.

5.3 Methods

5.3.1 Study area

The River Schelde is approximately 360 km long and has a drainage area of 21,863 km²; it originates on the plateau of Saint-Quentin in France, runs through Belgium and flows into the North Sea in The Netherlands. The Schelde Estuary is approximately 160 km long and has a complete salinity gradient from a tidal freshwater zone to marine, including extensive freshwater, brackish and salt marshes in its ecosystem (Fig. 5.1). It is a well-mixed estuary characterized by strong tidal currents (still prominently present during periods of high discharge (www.waterinfo.be)), high turbidity and a large tidal amplitude, up to 6 m (Seys et al., 1999). The estuary can be divided in two sections (upstream to downstream): the Zeeschelde (ZS), which spans 105 km from Gent to Antwerp (Belgium), and the Westerschelde (WS), which covers the 55 km from Antwerp to the mouth of the river at Vlissingen (The Netherlands)

(Table 5.1). Due to the funnel shape of the estuary, the maximal average tidal amplitude is reached in the freshwater tidal zone in the ZS. Further upstream, the river (Boven-Schelde) is obstructed by sluices and weirs, which reduce tidal action. Our study area comprised the estuary from Gent to Vlissingen, so it did not include any physical migration barriers.

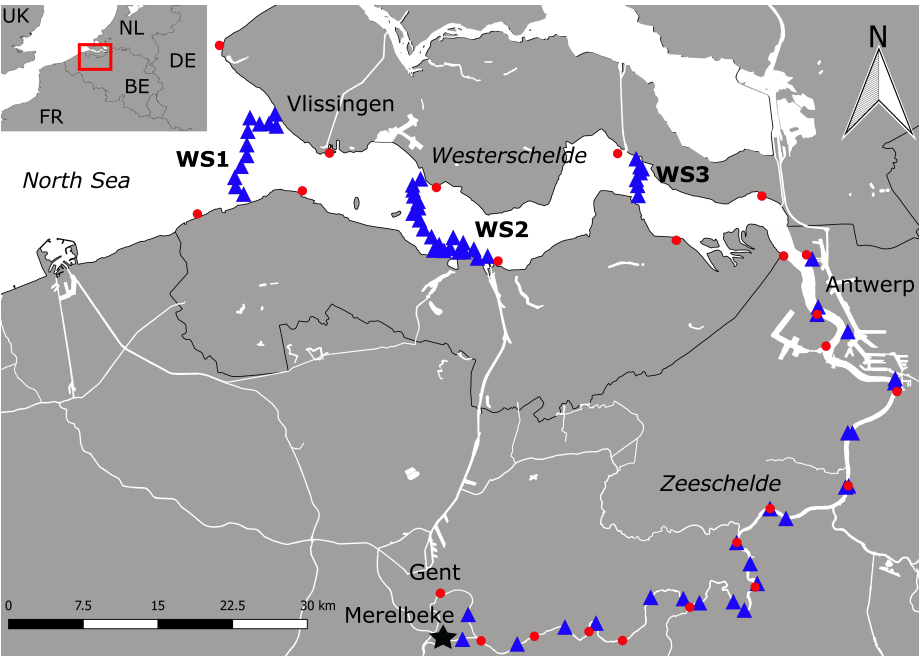


Figure 5.1: The Schelde Estuary comprises the Zeeschelde (Gent – Antwerp) and Westerschelde (Antwerp – Vlissingen). Acoustic listening stations are represented as blue triangles and the tidal measuring stations as red spheres. The black asterisk indicates the catch location in Merelbeke.

Table 5.1: Characteristics (length, width, average discharge and average tidal amplitude) of the Schelde Estuary.

	Zeeschelde	Westerschelde
Length (km)	105	55
Width (m)	50-1350	2000-8000
Average discharge (m^3/s)	100	120
Average tidal amplitude (m)	5.24	4.5

5.3.2 Tagging procedure

100 Eels were caught and tagged at the tidal weir in Merelbeke in the ZS during late summer and autumn (September-November) of three consecutive years (2015 till 2017) using double fyke nets (Fig. 5.1). Several morphometric features were measured in order to determine the eel maturation stage according to Durif et al. (2005): total length (TL, to the nearest mm), body weight (W, to the nearest g), the vertical and horizontal eye diameter (ED_v and ED_h respectively, to the nearest 0.01 mm) and the length of the pectoral fin (FL, to the nearest 0.01 mm) (Table S1). Only females were tagged, since males are smaller than the minimum size handled in this study (< 450 mm (Durif et al., 2005)). Eels of three different maturation stages were tagged: premigrant (FIII, $n = 51$) and the two migrant stages FIV and FV ($n = 21$ and $n = 28$, respectively).

The eels were tagged with V13 coded acoustic transmitters (13×36 mm, weight in air 11 g, frequency 69 kHz, ping frequency: 60-100 s; estimated battery life: 1021-1219 days (battery life time depended on specific transmitter settings) (Table S2) from VEMCO Ltd (Canada). After anaesthetising them with

0.3 ml L⁻¹ clove oil, tags were implanted according to Thorstad et al. (2013) with permanent monofilament. Eels recovered in a quarantine reservoir for approximately one hour and were subsequently released at the nearest ALS.

5.3.3 Acoustic network

Within the framework of the Belgian LifeWatch observatory, a permanent network of ALSs (VR2W, VEMCO Ltd, Canada) has been deployed since the spring of 2014 in the Schelde Estuary. In the WS, 39 ALSs are moored on marine navigational buoys in three arrays (from west to east: WS1: 12 ALSs, average interdistance: 1132 m; WS2: 21 ALSs, average interdistance: 909 m; and WS3: six ALSs, average interdistance: 800 m) (Fig. 5.1). The hydrophones were directed downward, as they were attached to a three-meter long chain with a weight at the end for stability. In the ZS, 25 ALSs are deployed from the river bank with coated wire, a weight to keep the ALS fixed on the bottom, and a buoy to direct the hydrophone upwards in the water column. The ALSs in the ZS are on average 4969 m apart. The detection range in both the WS and ZS varied from < 300 m to 1005 m and was highly dependent on current strength and wave action (unpublished data, but see Reubens et al. (2018) for the effect of environmental variables on the detection range in the Belgian part of the North Sea). Where the detection range was constrained by the current, we deployed an ALS on each side of the ZS river bank. Since in the WS we are dependent on navigational buoys, we could not reduce the distance between ALSs and therefore cannot guarantee full coverage at all times and all ALSs.

5.3.4 Data collection and processing

Of the 100 tagged eels, one was never detected and the other 99 were tracked between 16th September 2015 and 31st January 2018, resulting in a dataset with 302,824 detections (Fig. 5.2). The residency periods (i.e. the time between arrival and departure at an ALS) were calculated, which allowed to reduce the data by accumulating the number of detections during a fixed period of time. The delineation of these residency periods was based on three assumptions: we applied 1) an absence threshold of one hour (i.e. if the time between detections was ≤ 1 h, an eel was considered resident near that ALS), 2) a detection threshold of one detection (i.e. a single detection was considered to justify the presence of a tagged eel), and 3) a detection range of 1005 m (i.e. detections at two ALSs < 1005 m apart were assigned to one ALS since eels passing ALSs < 1005 m apart were detected at both ALSs at the same time due to the overlapping detection range). As such, the residency search resulted in detection intervals with arrival and departure times per eel at each ALS. Between an arrival and departure within the same detection interval, the number of detections and the residency period were calculated (Verhelst et al., 2018c).

Not all eels migrated, and those that did, did not always migrate upon tagging (Fig. S1). Therefore, an eel was considered migratory (and consequently a silver eel) when it travelled a net distance ≥ 20 km downstream during ≤ 40 days. Within that period, we selected the records from the most upstream till the most downstream station. The 20-km threshold is based on the maximum home range distance found for yellow eels (i.e. 18 km) (Verhelst et al., 2018d) plus two times the detection range of an ALS in the SE (i.e. the spatial error of the ALSs). The 40-days threshold is based on the finding that eels that did

not migrate ≥ 20 km downstream during that period, arrested their migration to proceed only during a next season. Indeed, applying the above assumption resulted in the selection of two migration phases for three individual eels: they arrested their migration, subsequently moved back upstream towards the vicinity of their catch location, and resumed migration two, ten and twelve months later, respectively (Fig. S2). For those three eels, we only took the second migration phase into account for analysis to avoid pseudo-replication. Data filtering, based on residency periods and migratory behaviour, resulted in the selection of 58 eels and a dataset of 104,737 detections over the period of 16th September 2015 till 2nd January 2018 (Fig. 5.2). All were detected in the ZS and 49 in the WS. Of the latter, 48 were detected at WS3, 36 at WS2 and 31 at WS1. The average migration distance per eel was 131 ± 35.8 km (range: 24-156 km) (Fig. S3) and the average tracking time (i.e. the time between the first and last detection of the considered migration phase) was 39 ± 20.2 days (range: 3-89 days) (Fig. S4).

To analyse if eels apply STST, the timing of high and low water were used (Levy and Cadenhead, 1995; Silva et al., 2017). Tidal data of the Schelde Estuary was obtained for Belgium and The Netherlands from the Hydraulic Information Centre (HIC) and Rijkswaterstaat (RWS), respectively. To account for the distances between the locations of the ALS and of the tidal measuring stations, a weighted average method was applied to estimate the precise moments of low and high water at the ALS. The closest upstream and downstream tidal measuring stations were assigned to each ALS. Based on the distances between these tidal stations and the ALS, weights were assigned to both tidal stations. When tidal data at the respective upstream or downstream tidal station was absent or of low quality at the time interval of interest, the next upstream or

downstream tidal station was chosen.

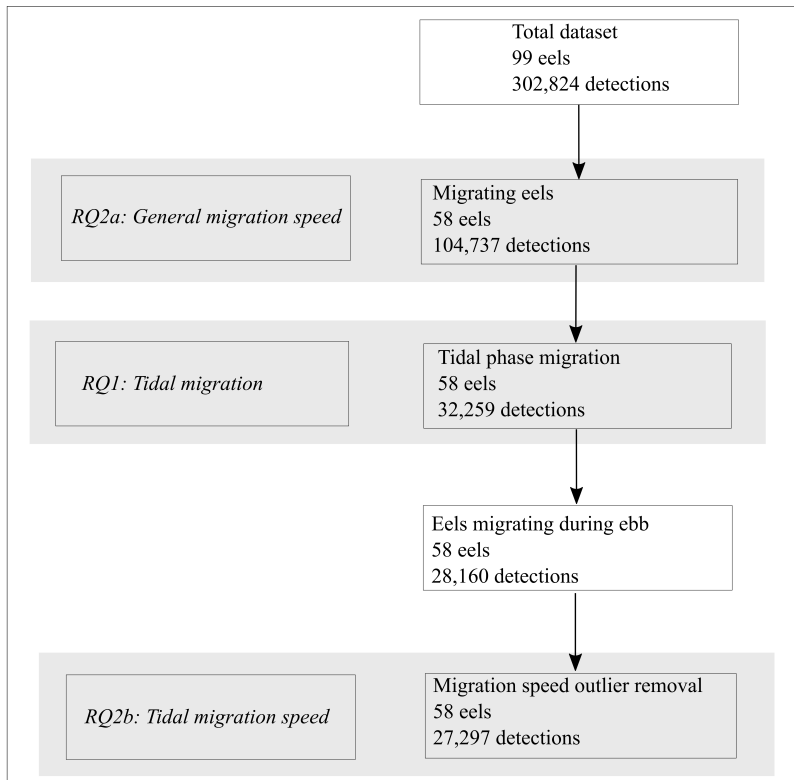


Figure 5.2: Illustration of the data selection flow with the number of eels and detections taken into account for each research question (RQ) (indicated with a grey frame) (RQ1: Do migratory eels apply STST?; RQ2a: What is the general migration speed in both the whole Schelde Estuary and the Zeeschelde and Westerschelde?; RQ2b: What is the migration speed during ebb in the Zeeschelde and Westerschelde?).

5.3.5 Data analysis

Tidal migration

To analyse if eels use STST, we determined what distance the eels travelled during each tidal phase (i.e. ebb or flood). Therefore, we calculated tidal movement intervals (TMIs) as the distance travelled per tidal phase, where upstream migration was regarded as a negative distance and downstream migration as a positive distance. Note that this was not possible for every inter-ALS movement, due to the resolution of our acoustic network. Movements occurring during different tidal phases were removed from the dataset as this data could not resolve whether eels effectively applied STST. This resulted in the removal of 72,378 detections; consequently, the remaining dataset contained 32,259 detections.

An eel was considered using STST if it moved downstream during ebb and showed no movement during flood. Therefore, the migration distances for ebb and flood were calculated per individual eel for each TMI. Consequently, eels were classified in two groups: those that exclusively migrated downstream during ebb TMIs (A) and those that showed downstream migration during flood TMIs as well (B). For the latter group, the records were further divided in downstream migration occurrences during ebb (Be) and other, i.e. up- and downstream migration occurrences during flood (Bf). Note that Be and Bf refer to records rather than to distinct individuals, and that a single eel thus yield records in both group Be and Bf. We applied a linear mixed effects model (transmitter ID as a random effect to account for autocorrelation) to test if group A (reference group) migrated over larger absolute distances than groups Be and

Bf (Zuur et al., 2009). We also added the dependent structure of the groups Be and Bf to the model as a random effect by assigning each eel of both groups a unique identifier. The nlme R package was used to conduct the linear mixed effects model (R Development Core Team 2017) .

Migration speed

Migration speed was calculated in three different ways. The first two methods consider general migration speeds and used the dataset without TMI extraction (i.e. 104,737 detections) (Fig. 5.2). First, we calculated the general migration speed over the whole study area as the time needed to cross the distance between the first and last detection.

Second, general migration speeds were calculated for the ZS and WS separately for three reasons: (1) migration speeds may differ between up- and downstream parts of the estuary (Bultel et al., 2014), (2) the morphology of both systems differs with the ZS being linear with one main channel and the WS having multiple channels, gullies and sand bars, and (3) the ALS networks in the ZS and WS each have a different setup (single points relatively close to each other vs distant arrays, respectively). The general migration speeds in the ZS and WS were calculated as the time needed to cross the distance between the two most distant ALS in each subarea. Since the data did not follow a normal distribution, a non-parametric Kruskal-Wallis test was applied to test for a significant difference in migration speed between the ZS and WS. Finally, the tidal migration speed was calculated as the time needed to complete the distances of the ebbing TMIs (i.e. group A and Be), again for the ZS and WS separately. The maximum reported migration speed found in literature was

1.93 m s^{-1} (Verbiest et al., 2012), consequently, speeds $> 2 \text{ m s}^{-1}$ were considered outliers and were removed from the dataset, resulting in a dataset of 27,297 detections (i.e. range outliers: $2.24\text{--}29.18 \text{ m s}^{-1}$) (Fig. 5.2). These outliers were likely due to the detection ranges of the ALSs (up to 1 km), resulting in an overestimation of the migration speed. To test if the tidal migration speed differed between the subareas, a linear mixed effects model was applied with transmitter ID as a random effect (Zuur et al., 2009); the nlme R package was used (R Development Core Team 2017) .

5.4 Results

5.4.1 Tidal migration

Of the 58 tracked migratory eels, 37 migrated exclusively downstream during ebb (group A), with an average (\pm SD) migration distance of $6590 \pm 5284 \text{ m}$ (range: $147\text{--}20877 \text{ m}$) per ebbing interval (Fig. 5.3). All 21 remaining eels (group B) showed both downstream migration during ebb (group Be) and up- and downstream migration during flood (group Bf); the downstream migration during ebb of group Be was not significantly different from that of group A: $9503 \pm 5672 \text{ m}$ (range: $341\text{--}22528 \text{ m}$) ($p > 0.05$; Table 5.2). The distances migrated during flood of group Bf ($-8860 \pm 6098 \text{ m}$ (range: $20069\text{--}2951 \text{ m}$)) did not differ significantly either from group A ($p > 0.05$; Table 5.2). Note that three and six of the Bf-eels exhibited upstream and downstream migration only once, respectively.

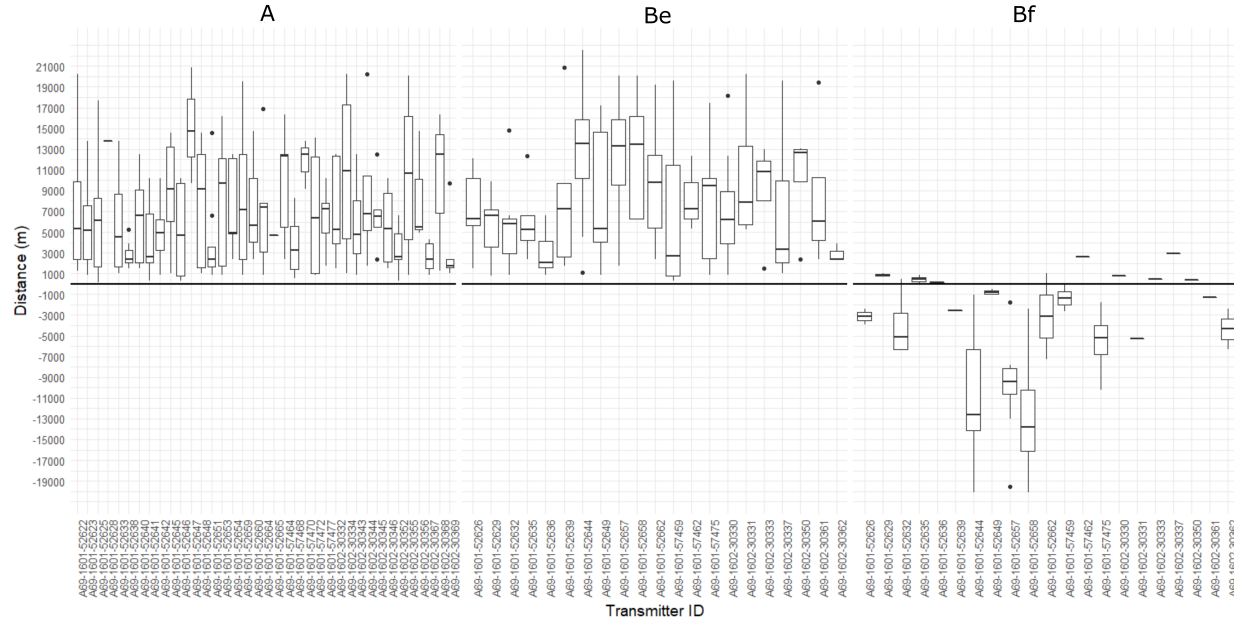


Figure 5.3: Migration distances (positive downstream, negative upstream) per eel (Transmitter ID) and group. Group A represents eels migrating solely during ebb while eels of group B migrate both during ebb (group Be) and flood (group Bf). The solid black line indicates the borderline between up- and downstream distance (i.e. distance zero).

Table 5.2: The output of the linear mixed effects model comparing downstream migration distances of eels exclusively moving downstream during ebb (group A; the reference group) with migration distances of eels migrating up- and downstream during flood as well (group B; showing both downstream migration during ebb (group Be) and up- and downstream migration during flood (group Bf)). The values, standard errors (SE), degrees of freedom (DF), t-values and p-values are indicated.

Fixed effects	Value	SE	DF	t-value	p-value
Intercept	6796	508	441	13.37	149e34
Group Be	1140	800	441	1.43	0.15
Group Bf	-769	901	441	-0.85	0.39

5.4.2 Migration speed

The average (\pm SD) general migration speed over the whole study area was $0.06 \pm 0.07 \text{ m s}^{-1}$ (range: $0.01\text{-}0.43 \text{ m s}^{-1}$). Eels migrated on average eight times faster in the WS compared to the ZS (KW-test, $\chi^2(1) = 70.07$, $p < 0.05$), with an average migration speed of $0.42 \pm 0.21 \text{ m s}^{-1}$ (range: $0.05\text{-}1.30 \text{ m s}^{-1}$) in the WS and $0.05 \pm 0.07 \text{ m s}^{-1}$ (range: $0.01\text{-}0.40 \text{ m s}^{-1}$) in the ZS (Fig. 5.4).

The average tidal migration speed did not differ significantly between the ZS ($0.93 \pm 0.34 \text{ m s}^{-1}$ (range: $0.08\text{-}1.87 \text{ m s}^{-1}$)) and WS ($0.95 \pm 0.41 \text{ m s}^{-1}$ (range: $0.04\text{-}1.64 \text{ m s}^{-1}$)) (linear mixed effects model, $DF = 305$, t-value = -0.50 , $p > 0.05$) (Fig. 5.4).

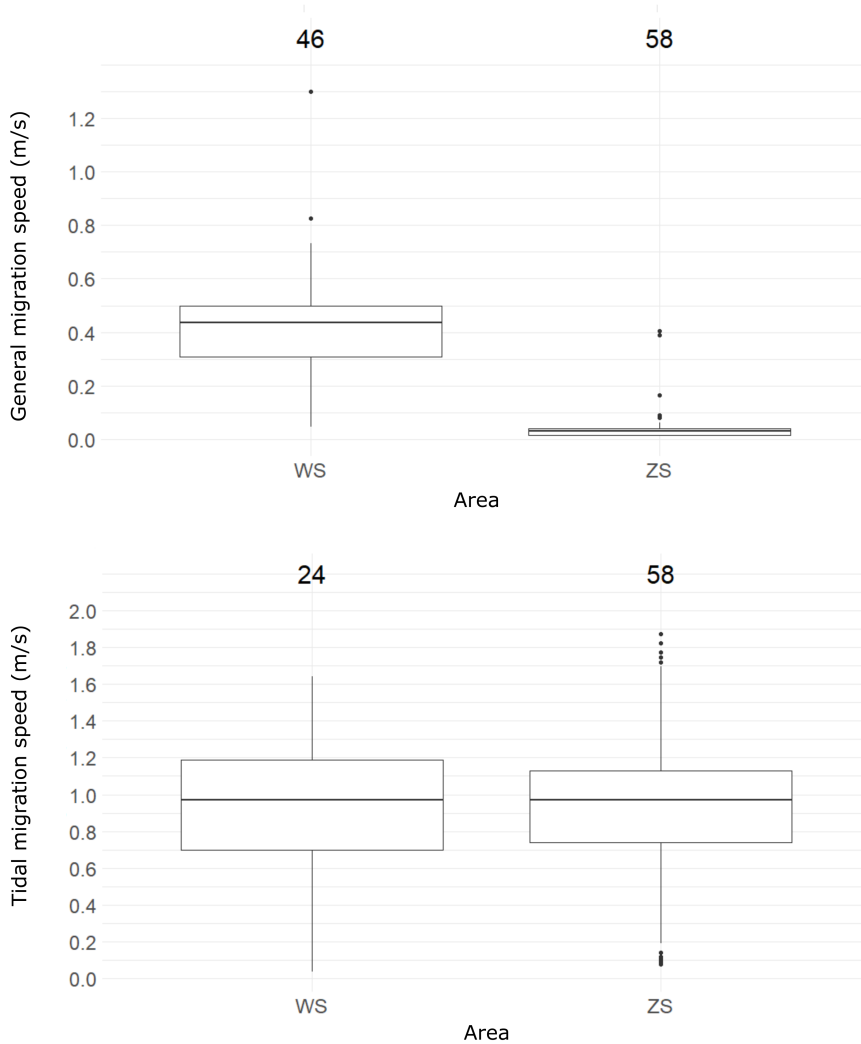


Figure 5.4: Boxplots representing the general (top) and tidal migration speeds (bottom) of the eels for the Westerschelde (WS) and Zeeschelde (ZS). Numbers of eels taken into account are indicated above the boxplots. Note that due to calculation of the tidal movement intervals and outlier removal, 22 eels were not taken into account to calculate tidal migration speed ($n = 24$) in the WS compared to the general migration speed ($n = 46$).

5.5 Discussion

5.5.1 Migration classification and detection efficiency

It is important to point out that not all tagged eels migrated, probably because in many cases tagged eels were still immature (Bultel et al., 2014; Stein et al., 2015). The majority ($n = 51$) of the tagged eels were in the premigratory stage (i.e. FIII) and apparently did not develop into migratory silver eels (i.e. FIV and FV) during the study period. As such, 40 of the 58 migrating eels were silver eels (FIV ($n = 15$) and FV ($n = 25$)) the moment of tagging. Yet, six FIV and three FV eels did not show migration behaviour. Other possible reasons why eels did not show migration behaviour include predation, tag expulsion or postoperative mortality. For instance, Thorstad et al. (2013) observed tag expulsion of 12% of the tagged eels six months after tagging. However, no mortality occurred during their study. Eel migration was also not always continuous, despite the definition of Kennedy (1985). However, when eels migrated a net distance ≥ 20 km downstream during ≤ 40 days, they almost always proceeded within the same migration season. Three eels did not and migrated back upstream to the vicinity of their catch location, indicating homing behaviour (Fig. S2) (Parker, 1995). These eels recommenced their migration two (i.e. the following spring), ten and twelve (i.e. the following autumn) months later. The reason for their arrested migration is unclear and may be attributed to an insufficient body condition or a change in the environmental triggers (Durif et al., 2002; Stein et al., 2015; Svedäng and Wickström, 1997).

Not all eels were detected till the downstream end of the ZS in Antwerp or

the arrays in the WS. Specifically, five eels (9%) were not detected in Antwerp and of the remaining 53 eels, five (9%) were not detected at WS3, 17 (29%) not at WS2, and 22 (38%) not at WS1. Eight eels were detected at WS3 and WS1, but not at WS2 and one eel was detected at WS2 and WS1, but not at WS3. Different factors may explain why migrating eels were not detected over the whole ALS network downstream of their release location: migration arrest, mortality due to predation, disease or fishing or an undetected migration through the three arrays in the WS as a consequence of, e.g., strong tidal currents, which can limit the detection range of the acoustic receivers (Reubens et al., 2018).

5.5.2 Tidal migration

This is the first study to unambiguously illustrate that European silver eels use STST, since the majority of the tagged eels exclusively migrated downstream during ebb. Moreover, never before has STST been observed for a large number of silver eels of any eel species. Passive acoustic telemetry allowed tracking of a large number of individuals for a long period of time and avoided potential biases from, e.g., a pursuing ship (i.e. disturbance of the environment), as was the case in active tracking studies on American and European silver eels, where only a handful of eels could be tracked for a limited period (McCleave and Arnold, 1999; Tesch, 1992, 1994). Prior to tracking, these previous studies kept the eels in holding tanks or laboratories for several days, while eels in our study were released immediately upon catching and tagging. Hence, acoustic telemetry and the methodology described in this study are a promising tool to apply to other diadromous species as well.

We want to note that tidal phases, based on the measured water levels, do

not always coincide with tidal currents as bottom friction and channel geometry can cause a phase shift between both (Van Rijn, 2010). Yet, previous studies analysing fish movement behaviour related to the tides did use water levels as well (Levy and Cadenhead, 1995; Silva et al., 2017). Nonetheless, future research linking animal tracking data to hydrological models may reveal substantial insight in animal movement behaviour, but requires innovative development of modelling and analysis tools.

Further, STST implies no movement during the inappropriate tide (McCleave and Arnold, 1999; Walker et al., 1978). Inherent to acoustic telemetry is the Eulerian nature of the data: fixed stations detect moving objects with spatiotemporal irregularity (Bruneel et al., 2018; Merki and Laube, 2012). Consequently, we can mainly conclude on movement and seldom on stationary events in an acoustic network with such a broad-scale resolution, unless the network is divided in zones delineated by ALSs serving as checkpoints, where eels can be considered resident if they did not pass a checkpoint (Trancart et al., 2018). High-resolution positioning systems with depth sensor tags may reveal additional insights, but could be constrained by logistics, spatial scale (such studies are often applied on a relatively small area) or the dynamics of the estuary. Pop-up satellite tags or data storage tags, resulting in Lagrangian data with regular temporal animal positions (i.e. both movement and stationary behaviour), can therefore provide further complementary insight into STST behaviour (Metcalf et al., 1990).

In this study, 37 eels migrated exclusively downstream during ebb-TMIs, while another 21 mainly did so. Consequently, the eels migrated substantially larger distances during ebbing tide compared to flooding tide, indicating that

they indeed used STST to migrate in an energetically efficient way through the estuary. This not only holds true for eels: salmonids and flounder also show STST (Jager, 1999; Levy and Cadenhead, 1995; Moore et al., 1995; Stasko, 1975). Estuaries play an important role in the life cycle of diadromous fish. The gradual transition from freshwater to the sea may be necessary to adapt to a wide range of salinities during their life cycle which accompanies physiological stress. Consequently, diadromous fish undergo gradual physiological changes (Arai, 2016; McCormick et al., 1998). When the transition is too abrupt, for example at a tidal sluice, this may have detrimental effects on the fitness of the fish. The canalization of rivers and especially the construction of tidal sluices has strongly reduced and even eliminated estuaries with the accompanying tides. This results in inaccessibility of important habitat, delays near tidal borders, and disorientation behaviour when diadromous fish abruptly enter the marine environment (Limburg and Waldman, 2009; Verhelst et al., 2018a,c).

STST also demonstrates that eels are able to distinguish the ebbing tide from the flooding tide and hence do not solely rely on water flow as a directional cue. It is plausible that silver eels detect specific cues in the ebbing tide, or that interactions between different variables trigger the migration. Glass eels have a good perception of the earth's magnetic field (Cresci et al., 2017), so it is possible that silver eels rely on such a system as well for orientation (Durif et al., 2013; Tesch, 1974). This illustrates the flexibility of the species, especially since it is plausible that at least a part of the migrating eels grew up in the upper reaches of the river, not encountering tides during the largest part of their life. Nonetheless, we did observe movement during flooding tide in 21 eels, the majority of which migrated with the ebbing tide for downstream migration. Various explanations for up- and downstream movement during flood

can be given, such as disorientation by the tide, predator avoidance, foraging behaviour due to insufficient energy storage, or a change in environmental migration triggers. It is not sure if these eels will contribute to the spawning population, but it illustrates that STST can be interrupted or may not even be vital to migrate through systems with tidal dynamics.

Although these results indicate silver eels use the ebbing tide to migrate, in non-tidal systems such as rivers and polders, it has been shown that an increase in discharge is an important variable (Bruijs and Durif, 2009; Buysse et al., 2015; Travade et al., 2010; Verhelst et al., 2018c; Vøllestad et al., 1986). Consequently, in tidal systems where the river discharge is stronger than the tidal currents during moments of, for instance, high rainfall, eels may use that increase in discharge to overcome flood events. Yet, the Schelde Estuary is a strong tidal system where discharge never exceeds the tidal forces (www.waterinfo.be; UAntwerpen pers. comm.). Consequently, it is unlikely that eels migrated against the flood due to a high discharge event.

The STST found in our study also followed temporal patterns in relation to the moon phase, circadian phase and tidal phase (Appendix). Downstream migration during ebbing tide mainly occurred around new and full moon, i.e. spring tide, and indicated that eels may time their downstream migration mostly during the periods with the strongest ebbing currents. Experimental studies found a relationship between eel migration and the moon phase (Boëtius, 1967; Edel, 1976; Hain, 1975; Tesch, 2003; Todd, 1981), but studies in a natural environment had hitherto failed to do so (Béguer-Pon et al., 2014; Vøllestad et al., 1986). A relationship of eel migration with the moon phase has previously been explained by the negative effect of light on eel behaviour,

suggesting that eels would be more active during new moon (Boëtius, 1967; Edel, 1976; Hain, 1975). Yet, we observed at least as many migratory movements during full as during new moon, contradicting the idea that the lunar effect merely relates to illumination (Hain, 1975). It may rather represent a tidal relationship, although we cannot exclude that direct illumination effects would be obscured in our data as a result of other factors such as cloud cover (LaBar et al., 1987; McGovern and McCarthy, 1992) and/or the high turbidity (Bruijs and Durif, 2009) of the Schelde Estuary. Indeed, we found substantial migration during daytime while silver eels are primarily nocturnal, a behaviour likely attributed to predator avoidance (Aarestrup et al., 2010; Travade et al., 2010; Verhelst et al., 2018c; Westerberg et al., 2007). Further, the majority of the TMIs started between 12% and 36% of the time duration of the ebbing tide after high water (0%). Generally, the strongest water flows are recorded during these moments of the tidal cycle (Meire et al., 2015). Specifically, during ebb, water flow increases from high water till two hours after high water (ca. 0%–28% relative to the tidal cycle) and then gradually decreases till low water to abruptly stop. However, note that the start of a TMI may not exactly reflect the onset of an eel's migration during a tidal phase; it is rather the first recording of an eel at an ALS, which does not exclude the possibility that the eel had started migrating at an earlier moment during the tidal phase.

5.5.3 Migration speed

Since eels mainly migrate during ebbing tide, a trade-off between migration speed (and consequently the timing of spawning) and energy expenditure may exist. Indeed, the general migration speed was relatively low (0.06 m s^{-1}) and

insufficient to reach the spawning sites in time, given they need to swim over 6000 km and spawning peaks in February (Righton et al., 2016). However, eels tend to migrate faster as they move downstream the estuary. (Bultel et al., 2014) found a higher migration speed in the lower parts of the Loire Estuary. Although we found that the tidal migration speeds in both the ZS (0.93 m s^{-1}) and WS (0.95 m s^{-1}) were similar during ebbing tide, overall migration speeds were considerably higher in the WS (0.42 m s^{-1} vs 0.05 m s^{-1} in the ZS). This indicates that eels migrate more consistently in the lower parts of the estuary and suggests that after a hesitant start of migration during which they may test for a sufficient body condition or environmental triggers, eels may finally 'decide' to migrate out (Hain, 1975). A gradient of increasing marine cues may support the more consistent migration further downstream the estuary. Nonetheless, the general migration speeds found in the SE and the WS and ZS separately are in line with the speeds observed in the marine environment ($0.03\text{-}0.54 \text{ m s}^{-1}$) (Huisman et al., 2016; Righton et al., 2016). This result therefore supports the hypothesis of a mixed migration strategy as proposed by Righton et al. (2016): a part of the eel population reaches the spawning grounds only during the following season.

Notably, it is plausible that some of the outliers (tidal migration speeds $> 2 \text{ m s}^{-1}$) were approximately real tidal migration speeds instead of outliers. Yet, further research with other techniques (i.e. with less spatial variation than the detection ranges of acoustic telemetry) can shed light on this topic.

5.6 Conclusion

The results of this study demonstrate that silver European eels use STST and underlines the importance of tides in eel migration. Hence, eels can make a distinction between ebbing and flooding tide, indicating that cues other than currents play a role in orientation. Apparently, tides help eels to migrate in a bioenergetically efficient way through estuaries, just like for other diadromous fish species such as salmonids and flounder. Therefore, restoration of estuaries, for example via tidal barrier management (Mouton et al., 2011b; Stuart and Mallen-Cooper, 1999), may not only aid recovery of the European eel population, but of diadromous fish species in general.

Chapter 6

Downstream migration of European eel (*Anguilla anguilla* L.) in an anthropogenically regulated freshwater system: Implications for management

Published as:

Verhelst, P.; Buysse, D.; Reubens, J.; Pauwels, I.; Aelterman, B.; Van Hoey, S.; Goethals, P.; Coeck, J.; Moens, T.; Mouton, A. 2018. Downstream migration of European eel (*Anguilla anguilla*) in an anthropogenically regulated freshwater system: implications for management. *Fisheries Research* **199**: 252 - 262.

For the supplemental material and appendices, we refer to the online version of the article: <https://doi.org/10.1016/j.fishres.2017.10.018>

6.1 Abstract

Connectivity between freshwater habitats and marine areas is heavily obstructed by anthropogenic structures (e.g. weirs, pumping stations, sluices...), leading to a high pressure on diadromous fish populations. A better understanding of fish migration behaviour in relation to these barriers is needed to take proper mitigation actions. We investigated the impact of migration barriers on downstream migrating European eel by tracking 50 acoustically tagged eels between July 2012 and March 2015 in a Belgian polder area. The study area was selected due to the presence of a wide range of migration barriers, such as two pumping stations, a weir and tidal sluices. These structures regulate the water level, resulting in discontinuous flow conditions. The results showed that migration was primarily nocturnal and discharge appeared to be the main trigger for migration in the polder. We also observed substantial delays and exploratory behaviour near barriers. Delays can have a serious impact on eels since their energy resources are limited for a successful trans-Atlantic migration. In addition, delays and exploratory behaviour can also increase predation and disease risk. The obtained knowledge can contribute to efficient management such as improved fish passage and guidance solutions.

6.2 Introduction

Worldwide, water levels of freshwater systems are controlled by structures such as pumping stations, weirs, dams and sluices. These structures hamper the movement of aquatic organisms, especially diadromous fish (Baumgart-

ner et al., 2009; Lassalle et al., 2009; Thompson et al., 2011). Polders are one particular ecosystem type where the role of barriers is crucial. A polder is an anthropogenic system where water is maintained at a lower level than outside the polder by pumping stations and weirs, which are two types of barriers that can negatively influence migration of both diadromous and potamodromous fish species (Buysse et al., 2014; Falke and Gido, 2006). Due to climate change, the associated rising sea level and a growing human population, pressure on dewatering systems is likely to intensify in the future, resulting in the development of more polders with their accompanying migration barriers (Beatty et al., 2014; Hannah et al., 2007; Hermoso and Clavero, 2011; Maceda-Veiga, 2013). In recent years, the importance of aquatic habitat connectivity has been recognized and is being addressed in management practices, resulting in developments to improve fish migration. As such, fish-friendly pump adaptations and fish passes have been developed to reduce mortality (Buysse et al., 2015; Clay, 1994). However, the efficacy of many presumably fish-friendly adaptations remains to be established (Boggs et al., 2004; Gowans et al., 1999; Keefer et al., 2004; Marmulla, 2001; Roscoe and Hinch, 2010). Next to mortality effects, pumping stations may also affect migration behaviour, resulting in delays or even migration stops. Consequently, delays or migration stops may result in a higher predation risk or reduced fitness and therefore contribute to the decline of a species (Marmulla, 2001).

In this study, we selected the European eel as a model species for downstream migrating fish encountering migration barriers. We used acoustic telemetry to reveal migration routes and link the detection data with biotic and abiotic data, thus providing knowledge about what variables trigger migration and whether eels encounter delays near barriers. This information can be

implemented in management measures to improve silver eel escapement rates.

Downstream migrating European eels were tracked from a polder area in Flanders (Belgium) into the Schelde Estuary (SE, The Netherlands). We selected the study area due to the presence of a wide range of migration barriers, such as two pumping stations (an Archimedes screw pumping station (APS) and a propeller pumping station), a weir and tidal sluices. Previous research showed silver eel mortality rates up to 19% at that particular APS (Buysse et al., 2015). We assessed five research questions related to downstream eel migration behaviour: (1) do eels take different migration routes; (2) does eel behaviour change significantly in the vicinity of barriers; (3) does migration follow a circadian pattern; (4) does migration start at a specific point in time; and (5) do environmental variables influence migration? The results of this study will support river and/or polder managers to facilitate downstream eel migration and hence contribute to the conservation of the eel stock.

6.3 Methods

6.3.1 Study area

The study area is comprised of three subareas, which are all part of the Schelde river basin: a polder (Flanders, Belgium), the Braakman pond (The Netherlands) and the SE (The Netherlands) (Fig. 6.1). The polder covers an area of about 200 km² and is drained via the Leopold Canal (LC). The LC is an unnavigable waterway of approximately 46 km long, 10-20 metres wide and one to four metres deep. It extends from Heist at the Belgian coast to Boekhoude.

Generally, it is a stagnant water system, but during dewatering, it can have a slow flowing current (on average $1.21 \text{ m}^3 \text{ s}^{-1}$ during this study period). Within the polder area, the LC connects different habitats such as ponds and small and large polder ditches with variable width and depth (Table 6.1). The Braakman is a brackish pond in The Netherlands, connected to the polder area in Belgium, with a mean chloride concentration of 3265 mg L^{-1} (range 580-8200 mg L^{-1}), a surface of approximately 2.05 km^2 and a depth up to 14 m. It is located at approximately one third of the SE (starting from the estuarine mouth) and functions as a transition area between the freshwater polder and the polyhaline zone of the SE. The latter is the lowest part of the Schelde river and leads to the North Sea. The funnel shaped estuary is approximately 55 km long with a variable width between two and eight km. It is characterized by intensive tidal action and strong currents and contains many sand banks, mudflats and salt marshes, resulting in a high turbidity.

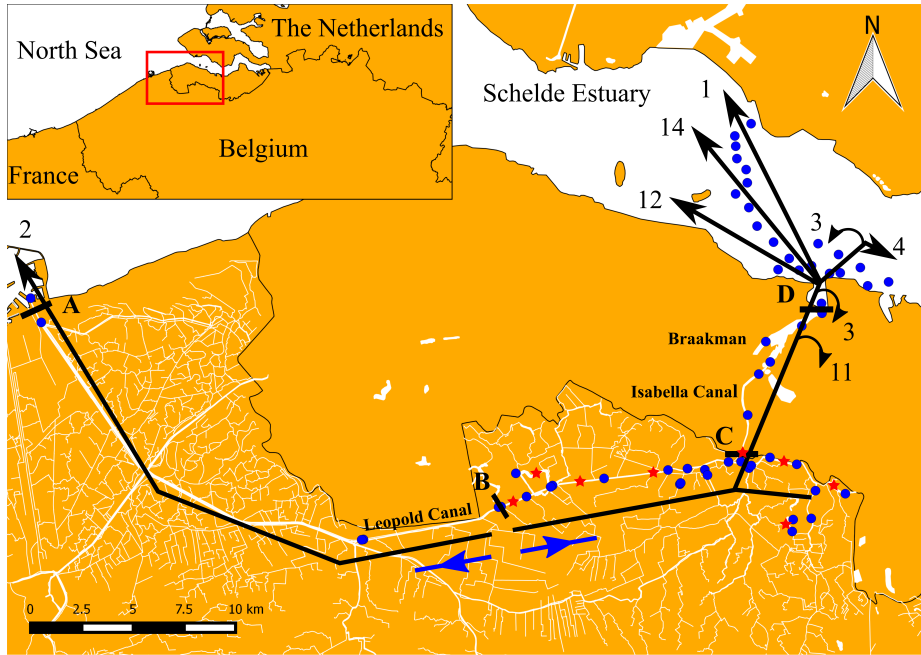


Figure 6.1: Study area with the Leopold Canal and its network of connected waterways (Belgium), the Isabella Canal, the Braakman pond (The Netherlands) and the Schelde Estuary (The Netherlands). ALSs are indicated as blue dots and catch-release locations as red asterisks. The four migration barriers within the study area are indicated with a black bar and bold letter: (A) the tidal sluice in Zeebrugge, (B) the low-head weir in Sint-Laureins, (C) the Archimedes Pumping station in Boekhoute, and (D) the tidal sluice with propeller pumps between the Braakman pond and the Schelde Estuary. The main current direction at each side of the weir is indicated with a blue arrow, while the migration routes of the 50 tagged eels are presented by black arrows. The numbers reflect the number of eels taking this specific migration route in the present study.

To dewater the system during high precipitation, water is pumped from the LC (1.40 m above sea level (a.s.l.)) into the Braakman pond (1.97 m a.s.l. in summer, 1.42 m a.s.l. in winter) via an APS in the Isabella Canal (Boekhoude), and flows gravitationally into the SE via a tidal sluice (Fig. 6.1). In case gravitational flow is insufficient to dewater the system, propeller pumps in the tidal sluice are used. In cases of exceptionally high precipitation, the polder system can also be dewatered towards Zeebrugge by lowering a weir in the LC (Sint-Laureins) (Fig. 6.1).

The APS has de Wit modifications to reduce fish mortality during passage, and along the APS a de Wit fishway is present (Buysse et al., 2015) (Fig. S1). The propeller pumps in the tidal sluice at the border between the Braakman pond and the SE do not have fish-friendly adaptations. In the western direction, connectivity from the polder area to marine areas is blocked by a low-head weir in Sint-Laureins and a tidal sluice in Heist at the freshwater - sea border.

Table 6.1: Depth and width of the different habitat types in the study area.

Type	Depth (m)	Width (m)
Canal	1-4	10-20
Polder pond	0.5-10	15-150
Large polder waterway	0.5-2	5-10
Small polder waterway	0.2 - 1	0.5-5
Braakman pond	1-14	200-750
Schelde Estuary	1-38	2000-8000

6.3.2 Tagging procedure

During the summer and autumn of 2012, 566 eels were caught in the polder and at the APS. From July to August 2012, 526 eels were caught with double fyke nets, which were placed in the LC, ponds and large polder ditches. At each location, four double fyke nets were placed and emptied during four consecutive days. Between the 5th and 16th of October 2012, another 40 eels were caught with two fyke nets attached to the outlet of two pumps of the APS during a survey to study eel mortality after passage (Buysse et al., 2015). Total length (TL, to the nearest mm) and body weight (W, to the nearest g) were measured and 50 eels (26 eels in the polder and 24 at the APS) were selected as large enough to tag with a mean length of $684 \text{ mm} \pm 75.76 \text{ mm}$ (range 556 mm - 874 mm) and mean weight of $683 \text{ g} \pm 260.23 \text{ g}$ (range 381 g - 1615 g). In this study, only females were tagged, since males are smaller than the minimum size handled in this study ($< 450 \text{ mm}$ (Durif et al., 2005)). Also note that the eels caught at the APS were checked for deformities and lesions prior to tagging.

In 2012, 46 eels were tagged with V13-1L coded acoustic transmitters ($13 \times 36 \text{ mm}$, weight in air 11 g, random delay between 80 s and 160 s, life time 1116 days, frequency 69 Hz) and four with V7-4L coded acoustic transmitters ($7 \times 22.5 \text{ mm}$, weight in air 1.8 g, random delay between 45 s and 95 s, life time 157 days, frequency 69 Hz) from VEMCO Ltd (Canada). After anaesthetising the eels with 0.3 ml L^{-1} clove oil, tags were implanted according to Baras and Jeandrain (Baras and Jeandrain, 1998). After recovery in a quarantine reservoir, eels were released at their catch location.

6.3.3 Acoustic network

An acoustic network of 56 ALSs (VR2W, VEMCO Ltd, Canada) was deployed in the harbour of Zeebrugge ($n = 1$), the polder area ($n = 27$), the Braakman pond ($n = 6$) and the SE ($n = 22$) (Fig. 6.1). The two ALSs in the Isabella Canal were considered part of the Braakman pond and detection data were handled accordingly. ALSs were moored at strategic locations to maximise the probability of detection: up- and downstream of each migration barrier, an ALS was deployed. Furthermore, ALSs were placed at each entry of a pond or polder waterway into the LC, while a uniformly distributed pattern in the Braakman pond was achieved. At the mouth of the Braakman into the SE, a double semi-circular array of ALSs was deployed in the SE, combined with one array stretching from the left to the right bank of the estuary. In the polder area and the Braakman pond, the stations were moored at the bank with weights and a small buoy. In this way, the hydrophone had an upward direction in the water column. In the SE, ALSs were moored at marine buoys, attached to a three-metre long chain with a weight at the end for stability. This resulted in downward directed hydrophones.

6.3.4 Data processing

Eels were tracked between 18th July 2012 and 25th March 2015 resulting in a dataset with 127475 detections. To reduce the dataset, the detections were accumulated for each eel at each ALS, resulting in detection intervals with arrival and departure times (VEMCO Users Environment software program, VEMCO Ltd, Canada). A one-hour absence threshold was applied: when an eel was

detected within an hour at the same ALS as the previous detection, it was considered within the same detection interval. If not, the detection was assigned to a new interval. Further, between an arrival and departure within the same detection interval, the number of detections and the residence time were calculated (Verhelst et al., 2018d).

Of the 50 tagged eels, 18 showed resident behaviour followed by downstream migration. As this study focused on downstream migration behaviour only, the data records with resident behaviour prior to downstream migration were removed from the dataset. To determine a sharp border between resident and downstream migration behaviour, a trajectory analysis was applied to each individual eel (Verhelst et al., 2018d). We used the method of Lavielle from the *adehabitatLT* package in R to divide an animal's trajectory in a resident and a migratory phase (Calenge, 2006) (Fig. S2). This method does not require discretisation in time and is based on residence time: it partitions movement segments based on homogeneous mean residence times (Lavielle, 1999, 2005; Barraquand and Benhamou, 2008).

6.3.5 Data analysis

In this study, different research questions were tackled with different data analyses. To determine the different migration routes and the impact of the migration barriers on eel behaviour, exploratory behaviour (i.e. non-directional movement) was included along with migration behaviour. To analyse the circadian pattern, when eels start to migrate, and what environmental variables influence migration, only downstream migration records were taken into account (hereafter called 'migration records'). After chronologically ordering the

data, a record was considered a migration record if the previous and next detection were at an ALS up- and downstream, respectively, or if the previous two detections were at two subsequent upstream located ALSs. For each analysis, assumptions were checked and data exploration was conducted following the protocol of Zuur et al. (2010).

Migration routes and impact of barriers on downstream migration behaviour

Recently, network-based tools have proven to be helpful in visualising the extensive datasets obtained by acoustic telemetry (Jacoby and Freeman, 2016). To reveal migration routes of individual eels, a unipartite network (i.e. 'one-mode' networks, see Jacoby and Freeman (2016) for more details) was created for each eel, consisting of nodes and edges. Nodes represented the ALSs with the total residence time of an eel at that ALS and edges the movements between them. The effect of barriers on migration behaviour was analysed in two ways (i.e. delays and exploratory behaviour) and only for the main migration route. For each node, the distance till the first downstream located migration barrier was calculated via QGIS (as there was no physical migration barrier downstream the SE ALSs, these records were excluded from the analysis of delays and of exploratory behaviour). For both delay and exploratory behaviour analysis, a Generalised Linear Mixed Model (GLMM) was applied with transmitter ID as random effect (i.e. as a proxy for individual variability). For analysing the delays, the total residence time per eel at each ALS was used as the fixed effect, while the total number of arrivals per eel at each ALS was applied as a fixed effect for the exploratory behaviour analysis. The distances between the nodes and the barriers were considered the fixed effect in both models. The residence

time data were continuous, consequently, a Gaussian GLMM with identity link was applied (Zuur et al., 2009). For exploratory behaviour analysis, we chose to perform a negative Binomial GLMM with log link, since this model is more robust against overdispersion compared to a Poisson GLMM (Zuur et al., 2009). We used the 'lme4' and 'lmerTest' package (Bates et al., 2014) in R (R Development Core Team 2017) to create the GLMMs and the 'blmeco' package to check the models for overdispersion: if the scale parameter was between 0.75 and 1.4, overdispersion was considered absent. The packages 'igraph', 'lubridate', 'matrix' and 'plyr' were used to represent the data as unipartite networks.

Circadian pattern

The number of migration records was summed per circadian phase. Consequently, four different circadian phases were determined and linked to each record in the dataset: dawn (start of civil twilight (i.e. when the geometric centre of the sun is six degrees below the horizon in the morning) to sunrise), day (sunrise to sunset), dusk (sunset to end of civil twilight (i.e. when the geometric centre of the sun is six degrees below the horizon in the evening) and night (end of civil twilight to start of civil twilight). Timestamps of sunset, sunrise and twilight were obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil/index.php>; coordinates: N51°16' E3°43').

Onset of migration

The onset of migration was simply determined as the month of the first migration record for each eel.

Environmental triggers of migration

Environmental data

To examine environmental triggers of downstream migratory behaviour, environmental variables were linked to the departure times per subarea (polder, Braakman pond and SE) in the dataset (Table S1). Environmental variables were selected based on data availability and on previous research (e.g. McCleave and Arnold (1999); Tesch (2003); Bultel et al. (2014); Buysse et al. (2015)). The 11 continuous variables were precipitation (mm), the APS and propeller pumps discharge ($\text{m}^3 \text{s}^{-1}$), water temperature ($^{\circ}\text{C}$) from the polder system and the SE, chloride concentration of the Braakman pond and the SE (mg L^{-1}), current velocity (cm s^{-1}) and direction (degrees) in the SE, day length (min) and air pressure (hPa). One variable was categorical: the gravitational flow at the tidal barrier between the Braakman pond and the SE (0: no gravitational flow; 1: gravitational flow). Pumping discharge, precipitation, water temperature and air pressure data were measured daily and obtained from the Flemish Environment Agency (www.waterinfo.be). Pumping discharge data were obtained daily by recordings from a metre at the APS, while water temperature and air pressure were measured near the APS (coordinates: N51°16'15.8" N E3°42'43.6"). Precipitation data was the average value over a large part of the study area (Fig. S3). There were two gaps of a couple of months in the water temperature data. To fill these gaps, data from a nearby canal were used (Ede canal; coordinates: N51°12'15.4" E3°26'22.3"). Both canals have a similar morphology and discharge regime, and showed a high correlation (0.98) in temperature regime. However, water temperature data for both canals differed significantly (two-sample t-test, $t = 2.98$, $p < 0.05$). Therefore, we applied a lin-

ear regression to obtain the relationship between the two datasets and fill in the gaps of the water temperature data of the studied polder area with the modified values of the nearby canal:

$$\text{water temperature LC} = 1.161941 \times \text{water temperature Ede canal} - 0.780858$$

Water level, pumping discharge, water temperature and conductivity data for the Braakman pond were obtained from the 'Scheldestromen Water Board'. Water levels up- and downstream of the tidal barrier were measured every 15 min; based on those data, it could be qualitatively determined when gravitational flow took place at the Braakman outflow (Fig. 6.1). As such, the variable gravitational flow was binomial: gravitational flow or no gravitational flow. However, during periods of high precipitation and no gravitational flow, pumps in the tidal barrier were activated to dewater the system (i.e. Braakman discharge; measured every 15 min). Conductivity data were measured once per month. These data were interpolated to link conductivity to the departure times of the eels. Water temperature of the Braakman was also logged once per month by the Scheldestromen Water Board. As the water from the upstream located polder flows into the Braakman, water temperature of the Braakman was highly similar to the water temperature of the LC: both datasets showed a high correlation ($\text{cor} = 0.99$) and a t-test indicated no significant difference (twosample t-test, $t = 0.22$, $p = 0.83$).

As such, the water temperature data of the polder was used for the analysis of downstream eel behaviour in the Braakman, because it has a higher resolu-

tion. The same air pressure and precipitation data of the polder area were used for the Braakman pond as the Braakman is located next to, and connected to the polder area.

Conductivity and water temperature of the SE were obtained from Rijkswaterstaat. These data were measured every 10 min near the Braakman outlet (coordinates: N51°20'38.8" E3°49'07.1"). Rijkswaterstaat also provided modelled data, with a 10-min accuracy, of flow velocity in the proximity of the ALS array (coordinates: N51°23'53.7" E3°43'15.7"). The same air pressure and precipitation data for the polder area were used for the SE.

The variable 'day length' was obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil/index.php>; coordinates: N51°16' E3°43'). In addition to the five environmental variables, one categorical explanatory variable was included, namely catch-release location habitat type (canal, polder ditch and pond).

Model development

For each subarea (polder, Braakman pond and SE), a model was developed with a different number of eels due to tagging locations and losses: the polder model ($n = 25$), the Braakman model ($n = 48$) and the SE model ($n = 34$) (Fig. S4).

For each model, the data was checked for outliers and homogeneity of variances. Thereafter, a collinearity analysis was conducted on the continuous variables (Zuur et al., 2010). For both the polder and Braakman pond model, a strong correlation (> 0.70) was found between water temperature and day

length; hence, the latter was removed from further analysis (Table S2 and Table S3) (Dormann et al., 2013). We chose to remove day length since previous research found that water temperature may play a role (Vøllestad et al., 1986). For the SE model, current direction and current strength were strongly correlated (Table S4). We chose to remove current strength, since we wanted to test for selective tidal stream transport, which is merely based on current direction (McCleave and Arnold, 1999). As such, for each subarea, different variables were selected for implementation in the GLMM (Table S1).

To determine what variables significantly contributed to silver eel migration, Random Forests (Hadderingh et al., 1999) and a Generalised Linear Mixed Model (GLMM) were applied. Both techniques use a different approach (classification versus regression, respectively), and results between the different models were compared. For each model, the response variable 'migration' was binomial: a record was considered migratory or not. To give an equal weight to migration and non-migration behaviour, bootstrapping was applied for the Braakman model to obtain the same number of records with and without migration (Mouton et al., 2010).

Random Forests (Hadderingh et al., 1999) is a widely applied machine learning technique (Breiman, 2001; Mouton et al., 2011a). Several studies have shown that RF often outperforms other state-of-the-art modelling techniques such as decision trees or support vector machines (Cutler et al., 2007; Fukuda et al., 2013). An important feature of RF is the availability of some measures to assess the importance of each variable and to detect outliers. In this study, the mean decrease in accuracy was calculated as an importance measure: after running the model, each variable obtains a value which represents the drop in

model accuracy when that particular variable is excluded from the model (i.e. the proportion of observations that will be wrongly classified if the variable is excluded). A more detailed description of the concept of RF can be found in Appendix A. We used the 'randomForest' package (Liaw and Wiener, 2002) of the R environment (R Development Core Team 2017), in which the default settings were applied.

GLMM, an extension of linear regression models, is a valuable technique to analyse relationships between explanatory variables and a response variable (Mouton et al., 2011a; Verhelst et al., 2016; Zuur et al., 2009). In this study, a binomial GLMM with a logit link was applied to assess the effects of the explanatory variables on silver eel migration. In addition, the significance of three random effects in the models was tested: year, month and tag ID, the latter as a proxy for individual variability. For each full model (i.e. the model with all explanatory variables), all possible combinations with the random effects were applied, including the single random effects. The model with the lowest Akaike Information Criterion (AIC) was selected to apply a stepwise backward model selection, again based on AIC: the polder model with the random effects 'month' and 'tag ID' had the lowest AIC (410.92), while the Braakman model with only 'month' as a random effect had the lowest AIC (659.03). For the SE, the model with 'tag ID' had the lowest AIC (378.61).

The kappa statistic (κ) was calculated to evaluate the RF and final GLMM models; the kappa index ranges between -1 and 1 (Cohen, 1960; Goethals et al., 2007; Mouton et al., 2010). We used the 'lme4' package (Bates et al., 2014) of the R environment (Team 2015) to create the GLMMs and the 'blme4' package to check the models for overdispersion: if the scale parameter is between 0.75

and 1.4, overdispersion is considered absent.

6.4 Results

6.4.1 Migration routes

Two migration routes were found: 48 eels (96%) migrated north via the APS in Boekhoude, while two (4%) migrated westward and reached the North Sea in Zeebrugge (Fig. 6.1, Fig. 6.2, Appendix B). The 48 eels arrived in the Braakman between summer (20th July) and winter (12th January). Of these, 37 (77%) reached the SE via the tidal sluice, while 11 eels (23%) were not detected outside the Braakman pond. Their detection signal was lost on average after 105 days (range 0-579 days). Ten of these eels had been tagged in the polder area, while one was tagged when intercepted in the APS, but swam upstream via the gravitational sluice after tagging and then migrated downstream through the APS into the Braakman. Notably, 11 (44%) of the 25 eels migrating through the APS (24 tagged in the polder and one tagged eel at the APS which swam upstream upon tagging) remained in the Braakman (Fig. S3).

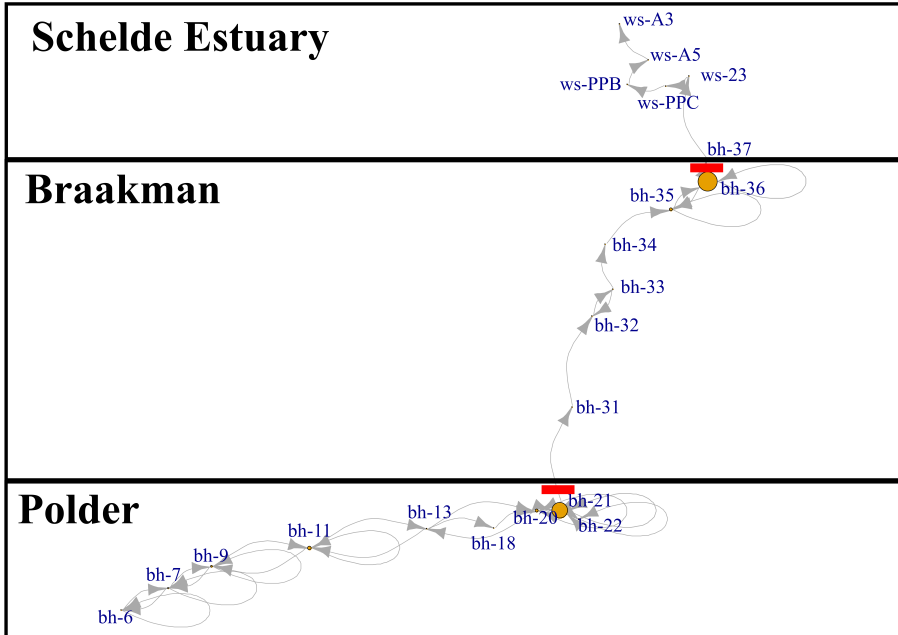


Figure 6.2: Unipartite network visualization of the trajectory of eel 29226. Each node represents an ALS (indicated by a yellow sphere with a location name) and the edges connecting the nodes are the movement patterns. The size of the node represents the total residence time for an eel at that ALS. The migration barriers are indicated with a red bar: in the polder the APS at Boekhoute and in the Braakman the tidal sluice with propeller pumps. Note that the thickness of the arrows does not indicate the number of movements between different nodes.

The eels detected in the SE departed from the Braakman between autumn (October 15th) and winter (January 20th), yielding a mean residence time of 26 days (0-102 days). None of them migrated from the Braakman into the SE

when the propeller pumps were active. In the SE, three of the 37 eels (8%) were detected only at the first ALS downstream of the tidal sluice in the Braakman, 27 (73%) migrated westward towards the North Sea, while seven eels (19%) swam eastward. The 27 westward migrating eels were detected on the array stretching from the left to the right bank of the estuary and revealed three different route choices in the SE (Fig. 6.1: 12 migrated along the left (southern) bank, 14 through the middle of the estuary and one swam across the estuary and then followed the right (northern) bank. Of the seven eastward migrating eels, three changed their swimming direction and were last detected near the mouth of the Braakman, indicating a westward migration direction. Together with the two eels detected in Zeebrugge, a total of 29 (58%) downstream migrating eels swam to the North Sea during this study.

6.4.2 Impact of barriers on downstream migration behaviour

Based on the individual unipartite network visualisations and statistical analyses, a significant higher residence time (Gaussian GLMM, estimated coefficient = -0.8246 ± 0.1169 , t value = -7.055 , $p = 1.09e-22$) and number of arrivals (negative binomial GLMM, estimated coefficient = -0.70723 ± 0.06327 , z value = -11.18 , $p < 2e-16$) was observed near the migration barriers (APS and tidal sluice) (Fig. 6.2, Fig. 6.3, Appendix B).

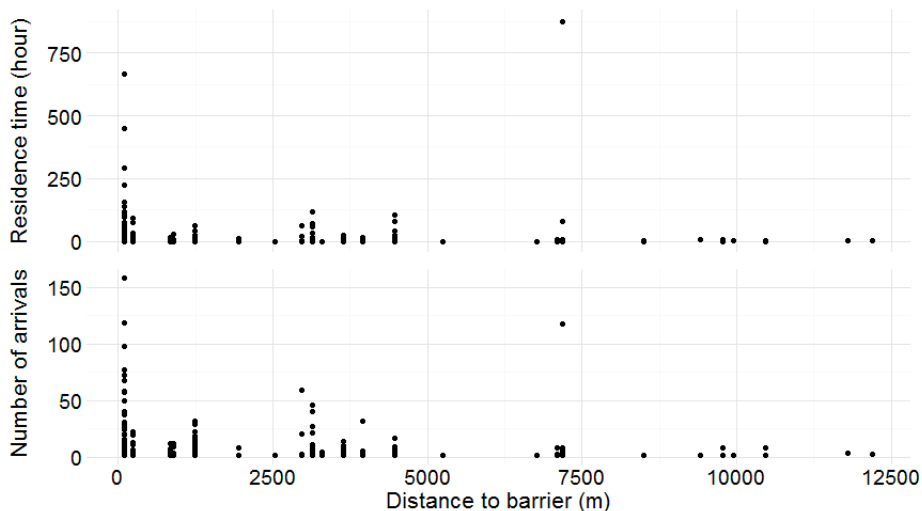


Figure 6.3: Residence time (upper) and number of arrivals (lower) as a function of upstream distance to a barrier. Both residence time and number of arrivals increased as the upstream distance to migration barriers decreased.

For the 25 eels migrating over the APS, the mean residence time at the ALS upstream of the APS was almost fourfold ($12.48 \text{ days} \pm 22.984 \text{ days}$ (range 0.01-91.74 days)) the mean residence time at the other ALSs located in the polder ($3.13 \text{ days} \pm 7.982 \text{ days}$ (range 0.01-61.6 days)). The same trend was found for the 48 eels reaching the Braakman. The mean residence time at the ALS upstream of the tidal sluice was over eight times as high ($84.47 \text{ days} \pm 130.058 \text{ days}$ (range 0.01-667.07 days)) compared to the other ALSs located in the Braakman ($10.44 \text{ days} \pm 63.594 \text{ days}$ (range 0.01-875.26 days)). Once in the SE, the mean residence time of the 37 eels ($8.05 \text{ days} \pm 84.756 \text{ days}$ (range 0.01-1141.22 days)) was intermediate to the mean residence times found at the

ALSs in the polder and the Braakman. Notably, the maximum residence time of 1141.22 days observed in the SE was attributed to an eel detected at the ALS downstream of the tidal sluice, which eventually migrated westwards. The second highest residence time in the SE was 89.57 days.

The average number of arrivals for the 25 eels in the polder was approximately the same at the ALS upstream of the APS and the other ALSs (5 ± 6.5 arrivals (range 1-22 arrivals) and 4 ± 7.6 arrivals (range 1–59 arrivals), respectively). For the 48 eels in the Braakman, the number of arrivals was more than sixfold higher at the ALS upstream of the APS (32 ± 34.7 arrivals (range 1-158 arrivals)) compared to the other ALSs in the Braakman (5 ± 10.3 arrivals (range 1-118 arrivals)). The number of arrivals for the 37 eels in the SE was relatively low compared to the polder and Braakman (3 ± 7.8 arrivals (range 1-95 arrivals)).

6.4.3 Circadian pattern

Overall, the majority of the migration records were obtained at night ($n = 413$), followed by day ($n = 71$), dawn ($n = 10$) and dusk ($n = 1$). This trend was found in each of the three subareas (polder, Braakman and SE) (Fig. 6.4), albeit that the proportions of observed migrations differed somewhat between subareas: almost fourfold the number of migration records in the polder were observed at night ($n = 82$) compared to daytime ($n = 22$), while in the Braakman, the number of migration records at night was over fifteen times higher ($n = 228$) compared to daytime ($n = 15$). In the SE, the difference in number of migration records between night and day was threefold ($n = 124$ and $n = 33$, respectively). Only four, two and four records were found during dawn in the polder, Braak-

man and SE, respectively, and only a single record was obtained during dusk, in the SE.

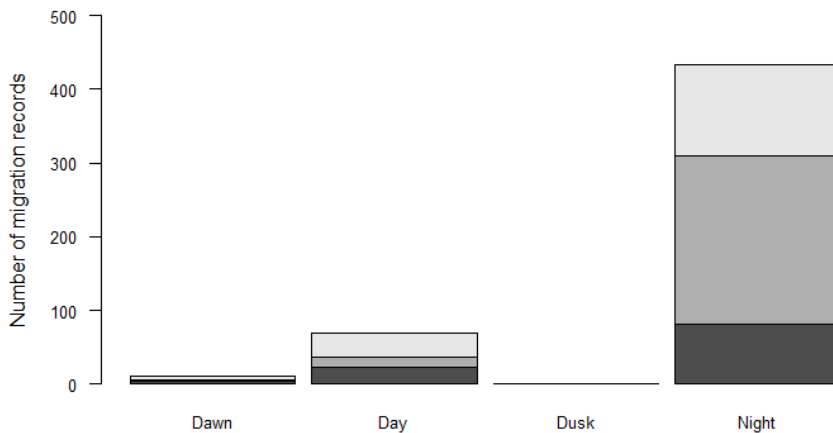


Figure 6.4: Number of migration records during the four circadian phases (dawn, day, dusk, night). Dark grey represents the number of records in the polder, medium-dark grey the Braakman and light grey the Schelde Estuary.

6.4.4 Onset of migration

The onset of migration of the tagged eels occurred between July 2012 and January 2015 (Fig. 6.5). Of the 50 tagged eels, 39 emigrated in 2012, seven in 2013, three in 2014 and one in 2015. The majority of the eels migrated in October ($n = 36$), while an equal number of emigrating eels was found in July ($n = 4$), Au-

gust ($n = 4$) and September ($n = 4$). Single eels started emigrating in December and January.

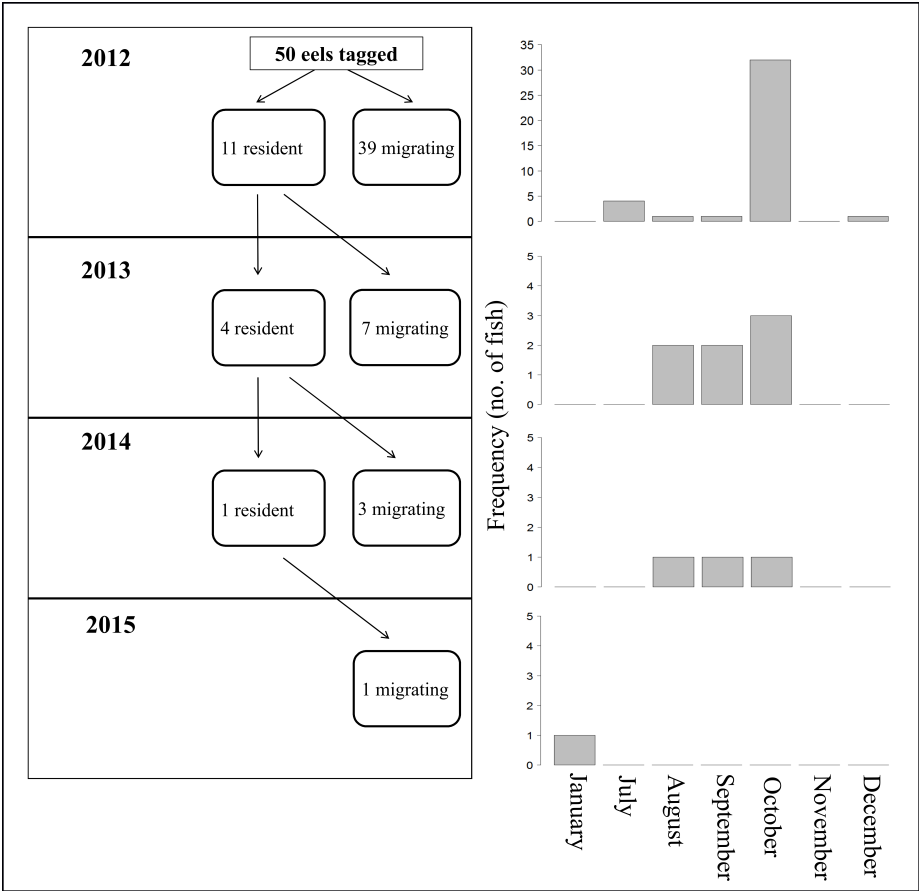


Figure 6.5: Schematic overview with the number of eels tagged in 2012 and the number of resident (i.e. eels residing in the polder area) and emigrated eels in the subsequent years. The boxplots indicate the number of eels emigrated per month over each year.

6.4.5 Environmental triggers of migration

In the polder, a significant positive relationship was found between discharge and downstream eel migration (GLMM, $\kappa = 0.55$, estimated coefficient = 0.1891 ± 0.0917 , z value = 2.062, $p = 0.0392$; Table 6.2). This result was confirmed by the RF ($\kappa = 0.16$), which also selected discharge as the most important variable affecting downstream eel migration (Table 6.3). Weak positive relationships were found between downstream eel migration in the Braakman and the variables chloride (GLMM, $\kappa = 0.14$, estimated coefficient = 0.00024 ± 0.00011 , z value = 2.103, $p = 0.0354$) and discharge (GLMM, $\kappa = 0.14$, estimated coefficient = 0.00019 ± 0.00011 , z value = 1.902, $p = 0.0572$). In addition, RF ($\kappa = 0.11$) selected discharge as the most important variable. Finally, no significant effect of any of the measured variables was found in relation to downstream eel migration in the SE. A slightly nonsignificant positive relationship with water temperature (GLMM, $\kappa = 0.57$, estimated coefficient = 0.3015 ± 0.1574 , z value = 1.916, $p = 0.0554$) was confirmed by the RF ($\kappa = 0.37$), which selected water temperature as the most important variable.

Table 6.2: The output of the GLMMs for each of the three subareas (polder, Braakman, Schelde Estuary) after stepwise backward selection. For each model, the number of migratory (N_1) and non-migratory (N_2) records taken into account is given, as is the AIC, κ and the selected random effect with the variance and standard deviation. For the intercept and the selected variables, the estimate, standard error (SE), Z value and P value are given.

Binomial GLMM (polder)				
$N_1 = 108$	$N_2 = 327$	AIC: 408	κ : 0.55	
Random effect:				
month (var = 0.98; SD = 0.99)				
year (var = 2.71; SD = 1.65)				
	Estimate	SE	z-value	p-value
Intercept	-0.66	0.62	-1.05	0.292
Discharge	0.19	0.09	2.06	0.039

Binomial GLMM (Braakman)				
$N_1 = 245$	$N_2 = 232$	AIC: 655	κ : 0.14	
Random effect: month (var = 0.06; SD = 0.25)				
	Estimate	SE	z-value	p-value
Intercept	-0.83	0.38	-2.18	0.029
Braakman discharge	0.0002	0.0001	1.90	0.06
Braakman chloride	0.0002	0.0001	2.10	0.04

Binomial GLMM (Schelde Estuary)				
$N_1 = 162$	$N_2 = 178$	AIC: 372	κ : 0.57	
Random effect: Transmitter (var = 5.09, SD = 2.26)				
	Estimate	SE	z-value	p-value
Intercept	-1.90	1.73	-1.09	0.274
Water temperature	0.30	0.16	1.92	0.055

Table 6.3: Order of importance of environmental variables in driving eel migration as obtained by the RFs and backward selection process for the GLMMs for the three different subareas (polder, Braakman pond and Schelde Estuary).

Order of importance	GLMM polder	GLMM Braakman pond	GLMM Schelde Estuary	RF polder (mean decrease in accuracy)	RF Braakman pond (mean decrease in accuracy)	RF Schelde Estuary (mean decrease in accuracy)
1	Discharge	Braakman chloride	WS water temperature	Discharge (104.00)	Braakman discharge (32.22)	WS water temperature (92.26)
2	Precipitation	Braakman discharge	Precipitation	Precipitation (64.10)	Precipitation (25.72)	Precipitation (69.49)
3	Water temperature	Air pressure	WS chloride	Water temperature (55.21)	Braakman chloride (17.91)	Air pressure (60.09)
4	Air pressure	Gravitational flow	Air pressure	Air pressure (50.59)	Water temperature (12.47)	WS chloride (57.17)
5		Precipitation	Current direction		Air pressure (8.81)	Day length (42.34)
6		Water temperature	Day length		Gravitational flow (1.65)	Current direction (10.27)

6.5 Discussion

6.5.1 Migration routes and impact of barriers on downstream migration behaviour

The main eel migration route in the polder was via the APS, as only two eels passed the low-head weir and migrated via the tidal sluice in Zeebrugge into the Belgian Part of the North Sea. The 48 downstream migrating eels taking the main migration route likely went through the APS and did not use the fishway, since Buysse et al. (2015) caught no tagged eels in the fishway from April 23rd 2012 to March 22nd 2013 (when 39 of the 50 tagged eels migrated) and concluded that the fishway did not mitigate downstream eel migration. Further, none of the tagged eels migrated from the Braakman into the SE when the propeller pumps were active (dewatering via the propeller pumps was exceptional and occurred for 49 days during the study period). Eels showed increased exploratory behaviour and delays at the APS and tidal sluice, much like they do when encountering hydropower stations (Jansen et al., 2007; Piper et al., 2013, 2017; Travade et al., 2010). In addition, although the Braakman was primarily dewatered gravitationally during the study period, creating a temporary migration barrier, the mean residence time for migrating eels in the Braakman was 26 days. During this residence time, exploratory behaviour was observed with significantly longer delays at the ALS near the tidal sluice. The discontinuous water flow resulting from the APS and tidal sluice may not be sufficient or last long enough for eels to effectively find their way to the estuary. This may disorient the eels, resulting in increased exploratory behaviour,

which could lead to temporary migration stops (Marmulla, 2001). Another plausible reason is that the APS and propeller pumps in the tidal barrier caused a lot of disturbance (i.e. noise, turbulence...), resulting in a certain reluctance of the eels to migrate further downstream (Sand et al., 2000).

In this study, 11 of the 25 (44%) eels migrating through the APS remained in the Braakman. A plausible explanation for this behaviour would be mortality after passage of the APS. However, the 44% observed in our study was much higher than the aforementioned 19% mortality reported by Buysse et al. (2015) at the same APS. Possible explanations for this higher percentage could be delayed mortality or a migration stop because of a reduced fitness after injury (Ferguson et al., 1989). Migration stops due to insufficient fat content (Svedäng and Wickström, 1997) are unlikely as the polder area is located close to the sea. Delays attributed to acclimatization are also implausible since eels can move frequently between fresh and salt water (Daverat et al., 2006) and progression rates are often faster close to estuaries (Aarestrup et al., 2010; Bultel et al., 2014). As such, the impact of pumping stations on fish migration could be underestimated in studies based on netting methods. Furthermore, piscivorous birds such as grey herons (*Ardea cinerea* L.) and cormorants (*Phalacrocorax carbo* L.) are abundant in the study area, so tag loss due to predation cannot be excluded. Adding to this, a commercial fisherman was active at the mouth of the Braakman, except between September and November when it is legally prohibited to catch eels in The Netherlands. Although the fisherman was able to identify and put back tagged eels, some eels may have gone unidentified.

Once in the SE, the eels did not encounter physical migration barriers on their way to the sea. Nonetheless, different migration behaviours were ob-

served (Fig. 6.1). The westward migrating eels ($n = 27$) selected three different migration routes (centre, left and right estuary bank), while a non-negligible proportion of eels ($n = 7$) even swam eastward. All these different types of behaviour may be the result of the dynamic processes in the SE: tidal movements, fluctuations in salinity, turbidity, oxygen and chemical composition of the water. The three migration routes of the westward migrating eels were probably attributed to different currents related to bathymetric channels and sand banks. Three eels were only detected at the ALS downstream of the tidal sluice. Since they emigrated during gravitational flow, injury is unlikely. They may have been predated by cormorants or have emigrated without being detected. Range tests in the Belgian part of the North Sea illustrated a mean detection range of 200 m, but this can be substantially reduced under conditions of strong currents or winds (Reubens et al., 2018).

For the seven eastward migrating eels, disorientation as a cause of tidal currents may have occurred, although some eels migrated eastward when tidal direction was westward. It is possible that the eels were not fit anymore for migration due to the delays or were still recovering from injuries inflicted on them at the APS. Eels can postpone their migration in estuaries, probably due to insufficient fat reserves (Aarestrup et al., 2008; Parker and McCleave, 1997). As such, eels might have swam eastward up the estuary to proceed feeding until they were fit enough again for migration. However, eels migrating westward could equally turn into a semi-yellow stage (Svedäng and Wickström, 1997). This would imply that the silvering process is still reversible in late freshwater - early estuarine conditions (Svedäng and Wickström, 1997). Despite the good coverage by the ALS arrays in the estuary, we cannot exclude that the eastward migrating eels later migrated to North Sea without being detected on the array

stretching from the left to the right bank due to the dynamic currents in the SE (Reubens et al., 2018). Specifically, three of the seven eastward migrating eels changed their migration direction westwardly, but they were not detected on the ALS array stretching from the left to right SE bank.

6.5.2 Circadian pattern

Eels primarily migrated at night, which is in accordance with previous studies (Aarestrup et al., 2008, 2010; Brown et al., 2009; Travade et al., 2010; Vøllestad et al., 1986) and with the general assumption of predator avoidance (Westerberg et al., 2007). Notably, nocturnal downstream migration was more pronounced in the Braakman than in the polder. A plausible explanation might be that the large numbers of cormorants (tens to hundreds) in the Braakman result in a higher predator avoidance effect in the eels and therefore a more pronounced nocturnal activity. Consequently, although gravitational flow can occur twice every 24 h since it is dependent on low tide, the majority of the eels may only be able to pass the tidal barrier at night.

Especially in the SE, however, diurnal downstream migration also occurred, more frequently so than in the polder and Braakman. This is likely a consequence of the high turbidity of the SE (Bultel et al., 2014). Indeed, day-time activity of resident eels has been reported during periods of increased turbidity and/or during overcast weather (Baras et al., 1998; LaBar et al., 1987; McGovern and McCarthy, 1992).

6.5.3 Onset of migration

Due to the large distribution range of the European eel, the onset of downstream migration varies between catchments depending on the travel distance to the spawning grounds (Tesch, 2003). Considerable variation also exists within catchments: eels living in upstream locations migrate earlier (Tesch, 2003). Nonetheless, downstream migration generally takes place in autumn (September to December) (Righton et al., 2016; Tesch, 2003; Vøllestad et al., 1986). Despite the relatively small catchment area (200 km²) studied here, substantial variation in onset of migration was observed (covering a period of six months (July - January), but with a clear peak in October. However, the 24 eels caught at the APS in October were considered intercepted downstream migrating eels, so the onset of their migration may have occurred before October. This is in line with a 'parallel' study by Buysse et al. (2015) at the APS of the LC, where the highest eel numbers were caught in July, October and December 2012, with a main peak in October. The broad period of six months indicates that mitigation actions for downstream migrating eels may need to cover a broader time window than the commonly referred autumn months.

6.5.4 Environmental triggers of migration

Discharge appeared to be the primary trigger of migration in the polder, corroborating observations at the APS of the LC, where eels passed mostly during high discharge events (Buysse et al., 2015), as well as earlier studies (Travade et al., 2010; Vøllestad et al., 1986). It is generally assumed that eels migrating downstream take the energetically most favourable route to their spawning

grounds (van Ginneken and van den Thillart, 2000) as they do not feed during migration (Chow et al., 2010; Tesch, 2003) and rely on their fat reserves for both migration and spawning. As such, swimming along with the current gives the eel an energetic advantage.

In the Braakman, a weak, but significantly positive relationship of migration behaviour with chloride concentration was found. It is possible that eels used saltwater intrusions during gravitational flow to find their way to the estuary. In contrast to the polder, no significant relationship with discharge or gravitational flow was found. The discharge and gravitational flow probably were not substantial or did not last long enough for eels to show a significant response. This was confirmed by the long residence time of eels in the Braakman.

It is still unclear which estuarine cues guide eels to the sea; probably a hierarchical interaction of different directional cues is used (Barbin et al., 1998). In this study, a positive relationship between water temperature and migration was revealed by the statistical models. In autumn and winter, the North Sea water is warmer than that of the SE; no water column stratification is present in the SE. It is therefore plausible that, once in estuarine conditions, eels positively react to higher water temperatures for guidance to the sea. Furthermore, it has been shown that eels use selective tidal stream transport to migrate in an energetically favorable way (Béguier-Pon et al., 2014; McCleave and Arnold, 1999; Parker and McCleave, 1997), but no such relation was found in our study¹. However, we cannot exclude the use of selective tidal stream transport, be-

¹At the time this research was conducted, the information revealed by Chapter 5, which was performed later, was not yet available. To date, we do have an indication of STST for European eels.

cause the estuarine behaviour comprises only the initial encounter of the eels with the tidal environment, and they may require some time to 'adapt' to the tidal rhythm (Barbin et al., 1998).

6.5.5 Management recommendations

Understanding and mapping eel migration routes from inland waters to the sea is extremely important in view of the critically endangered status of the European eel, the population of which is still declining (Dekker, 2016). The goals of the European Eel Regulation, i.e. that 40% of the emigrating eels should reach the sea, are still not met (Dekker, 2016). This study analysed downstream eel migration behaviour from a freshwater polder into an estuary. We found that 64% of the tagged emigrating eels reached estuarine and marine areas during the study period, confirming the negative impact of migration barriers on eels. The barriers not only affect eels directly via mortality and injuries (Buysse et al., 2015), they also cause significant delays and exploratory behaviour, likely due to discontinuous flow conditions. These negative impacts of barriers on downstream eel migration may substantially impact the eels' chances to contribute to the spawning population (Brown et al., 2009; Jansen et al., 2007; Piper et al., 2013, 2015, 2017; Travade et al., 2010).

Polder areas and pumping stations exist all over the world, and many are under construction to deal with climate change impacts and sea level rises, creating migration barriers to diadromous fish species like the eel. As diadromous species show seasonal spawning migration under specific conditions, a possible cost-effective management measure could be 'temporal barrier management' (Piper et al., 2013). Barriers could temporarily be removed when migra-

tion conditions are met, during so-called environmental windows, a concept commonly applied with dredging operations (Suedel et al., 2008) and recently also to improve glass eel colonization of freshwater systems (Mouton et al., 2011b). In addition, if effective fish-friendly adaptations to pumping stations are not present, gravitational flow should be stimulated during the environmental windows.

Since eels in freshwater systems mainly migrate at night and during periods of high discharge, a stimulation of gravitational flow under such conditions could probably increase the number of eels reaching the sea and contributing to the spawning population. Notably, the duration of this mitigation action needs to be sufficient so that a continuous flow over a longer time period is generated. However, the duration may be dependent on the study area and requires further research.

Indeed, since the end of 2015, Flemish water managers (Flemish Environment Agency and Waterwegen en Zeekanaal NV) have been taking actions to stimulate gravitational flow: the weir in Sint-Laureins has been lowered, such that the polder can be dewatered through gravitational flow towards Zeebrugge. However, during periods of high precipitation (especially autumn and winter), dewatering towards Zeebrugge is insufficient, leading to activation of the APS in Boekhoute. To stimulate gravitational flow, a possible mitigation action would be to reduce the water level of the Braakman below the level of the polder in autumn.

Chapter 7

European silver eel (*Anguilla anguilla* L.) migration behaviour in a highly regulated shipping canal

Published as:

Verhelst, P.; Baeyens, R.; Reubens, J.; Benitez, J.-P.; Coeck, J.; Goethals, P.; Ovidio, M.; Vergeynst, J.; Moens, T.; Mouton, A. 2018. European silver eel (*Anguilla anguilla* L.) migration behaviour in a highly regulated shipping canal. *Fisheries Research* **206**: 176 - 184.

For the supplemental material, we refer to the online version of the article:
<https://doi.org/10.1016/j.fishres.2018.05.013>

7.1 Abstract

Among the many man-made structures that facilitate shipping, navigable canals take an important position. These canals may offer energetically favourable migration routes for diadromous fish, but they may also obstruct fish migration, for instance at shipping locks. Because the use of shipping canals by, and their effects on, migrating fish remain unknown, we assessed whether these canals can play a significant role in the migration of the critically endangered European eel. Only one third of 70 acoustically tagged silver eels completed migration through a shipping canal, and did so at a very low pace (average $< 0.06 \text{ m s}^{-1}$) due to delays at shipping locks and most likely also due to the disruption of water flow. These delays may come at an energetic cost, hampering the chances of successful migration. Knowledge on the impact of shipping canals on diadromous fish is crucial for proper management regulations. For instance, the observation that eels mostly migrated at night and during spring and autumn can support water managers to define adequate measures to improve eel migration in shipping canals.

7.2 Introduction

Canals for navigation and irrigation are among the most anthropogenically altered water bodies worldwide (Vitousek et al., 1997). Not only are they widely distributed, their number is likely to increase in the future due to climate change and a growing human population (Hannah et al., 2007). Canals are commonly characterised by a low structural variability (e.g. concrete em-

bankments without riparian vegetation) with shipping locks, weirs and turbine stations, resulting in a regulated water flow. In addition to navigation, canals support industrial water management by facilitating water withdrawal and waste water disposal. It has already been shown that shipping canals may have a negative effect on local freshwater fish communities (Arlinghaus et al., 2002; Wolter and Arlinghaus, 2003). Such negative effects can be direct (e.g. shear stress, ship waves, dewatering and backwash...) or indirect (e.g. habitat fragmentation and simplification, loss of spawning and nursery habitats...) (see Wolter and Arlinghaus (2003) for an extensive review). Although the impact of shipping canals on non-migratory fish species has been extensively studied (Arlinghaus et al., 2002; Wolter, 2001; Wolter and Arlinghaus, 2003), knowledge on their effects on diadromous fish species remains scant. Shipping canals generate threats for diadromous fish species: structures such as shipping locks, weirs and turbine stations, as well as the regulated water flow, may hamper migration behaviour (e.g. by disorientation). However, shipping canals may also provide alternative opportunities such as new migration routes, by connecting river basins or creating shorter migration routes to the sea. Depending on the impact of these canals on fish migration, proposed management measures could for instance include adjusted flow regulation or mitigation measures at turbine stations and shipping locks. A group of diadromous fish species of particular interest, are catadromous anguillid eels, as species have declined tremendously during the last decades. The decline of the European eel, for instance, is the consequence of various causes, such as migration barriers, habitat deterioration, pollution, human-introduced parasites, fisheries and changes in ocean climate (Buysse et al., 2014; Feunteun, 2002; Køie, 1991; Miller and Tsukamoto, 2016; Moriarty and Dekker, 1997). Habitat fragmentation by

migration barriers, preventing the downstream migration of silver eels and upstream migration of glass eels, is regarded as an important bottleneck for this species (Mateo et al., 2017; Mouton et al., 2011b). A changed flow regime may also negatively impact silver eel migration, especially since water flow is considered a crucial factor for eel migration (Travade et al., 2010; Verhelst et al., 2018c; Vøllestad et al., 1986). To bridge this knowledge gap, we investigated the downstream migratory behaviour of the European eel in a shipping canal.

European silver eel migration behaviour has been studied in various systems such as rivers (Piper et al., 2015; Stein et al., 2015; White and Knights, 1997; Winter et al., 2007), polders (Buysse et al., 2015; Verhelst et al., 2018c), estuaries (Aarestrup et al., 2008; Bultel et al., 2014) and the marine environment (Aarestrup et al., 2009; Amilhat et al., 2016; Huisman et al., 2016; Righton et al., 2016; Wysujack et al., 2015), but migration behaviour in large canals with shipping locks is still underexplored. We tracked 70 silver eels in the Belgian Albert Canal using acoustic telemetry. This shipping canal connects the two largest river catchments of Belgium (i.e. Schelde and Meuse), resulting in different potential migration routes.

We assessed three research questions related to silver eel migration behaviour in the Albert Canal: (1) are eels able to migrate out of the system, (2) are they delayed in their migration, and (3) how does their behaviour relate to eel migration behaviour in other systems?

7.3 Methods

7.3.1 Study area

The Albert Canal is ca 130 km long, 86 m wide, 5 m deep and functions as a shipping route between the rivers Schelde (Antwerp) and Meuse (Liège) for ships up to 12,000 tonnes, illustrating its economic importance. Secondary canals are connected to the Albert Canal for irrigation and navigation purposes (mainly recreational navigation): Zuid-Willemsvaart, Canal Briegden-Neerharen, Canal Beverlo, Canal Dessel-Kwaadmechelen, Canal Bocholt-Herentals and Canal Dessel-Turnhout-Schoten (Fig. 7.1).

The Albert Canal is fed by the Meuse, with which it has an open connection (i.e. no shipping locks are present). The water level is kept constant by the weir at Monsin, at the junction between the Meuse and the Albert Canal. Part of the water is used to fill the shipping locks in Lanaye and Wezet, after which the water runs back into the Meuse (see Fig. S1 for details regarding the different connections of the Albert Canal with the Meuse). The other part is used to water the Albert Canal and has an average water flow of $9 \text{ m}^3 \text{ s}^{-1}$ in Genk (Baetens et al., 2005). The Albert Canal is divided in seven navigation sections (A-G) by six shipping lock complexes (each complex consists of three shipping locks) without weirs (from Schelde to Meuse, these are located at Wijnegem, Olen, Ham, Hasselt, Diepenbeek and Genk) to overcome the 56-m head drop. During the 27-month study period (3rd September 2014 till 20th December 2016), the majority of the ships came from the harbour of Antwerp and were transported via the shipping locks in Wijnegem (Table S1). The num-

ber of transported ships gradually decreased over the shipping locks towards the Meuse, since the destination of some ships was along the Albert Canal, after which they returned to Antwerp. Only in 2014 a substantial number of ships was transported over the shipping lock in Genk (De Vlaamse Waterweg nv, unpublished data). Although the net flow direction is towards the Schelde, shipping lock operation and accompanying navigation result in a highly disrupted flow regime. Opening the locks happens relatively fast (i.e. within 15 min), resulting in back-and-forth moving waterfronts in the canal sections and a water flow that temporarily differs between sections. Notably, section G has the lowest water flow of the system because the water mass is distributed over the docks (Hydrological Information Center, pers. comm.). The shipping locks operate from Monday morning 6 a.m. till Saturday evening 10 p.m, and remain inactive on Sundays and holidays. Due to limitations of nocturnal navigation, the locks mainly operate during daytime. Specifically, for the period November 2014 till January 2016, 66% of shipping lock operations occurred during daytime compared to 30% at night. During dusk and dawn, shipping locks were both operational for 2% each of the time (shipping lock operation data obtained by De Vlaamse Waterweg nv). On top of shipping lock filling, the water manager discharges water via an underground canal when the Meuse discharge is high (especially in winter and spring). However, we do not have data about that activity. Based on a fish monitoring survey from 2012 till 2015, the Albert Canal is characterised by a low fish biomass, ranging from 12.9 kg ha⁻¹ to 24.2 kg ha⁻¹ (Visser and Kroes, 2016). The diversity ranges between 15 and 18 species. The majority of the species are eurytopic, such as roach (*Rutilus rutilus* L.), bream (*Abramis brama* L.) and perch (*Perca fluviatilis* L.). Note that especially roach and bream are stocked for recreational angling purposes.

Rheophilic and phytophilic species are scarce, while the numbers of invasive round goby (*Neogobius melanostomus* P.) are increasing over the years.

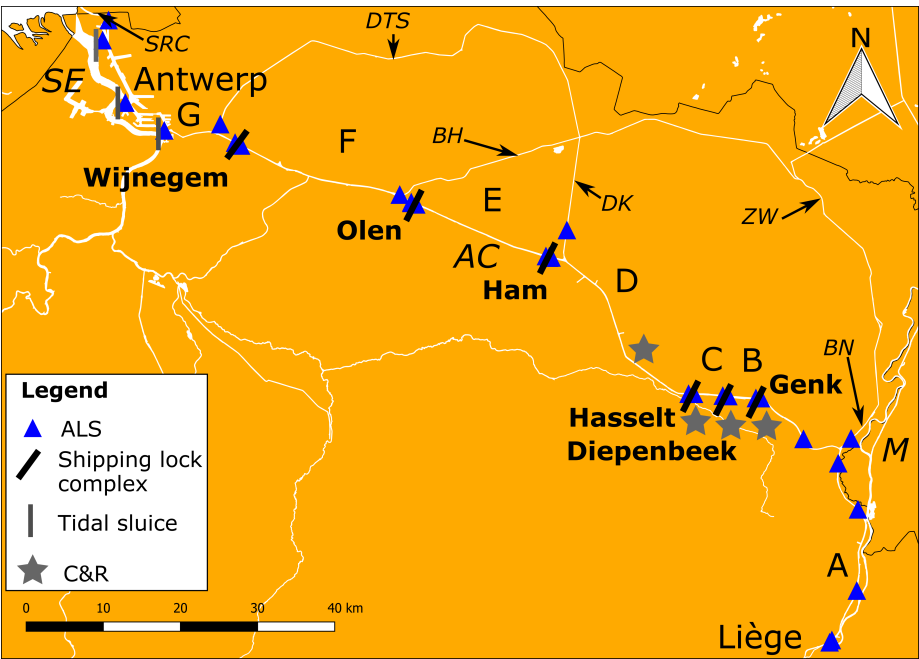


Figure 7.1: Study area with the Albert Canal (AC) and its network of secondary canals: ZW (Zuid-Willemsvaart), BN (Canal Briegden-Neerharen), DK (Canal Dessel-Kwaadmechelen), BH (Canal Bocholt-Herentals) and DTS (Canal Dessel-Turnhout-Schoten). Also the Schelde-Rijn Canal (SRC) is indicated. The Albert Canal connects the Schelde Estuary (SE) in Antwerp (tidal sluices indicated by grey bars) with the Meuse river (M) in Liège. The Albert Canal is divided in seven canal sections (A-G) by six shipping lock complexes (indicated by black bars; Genk, Diepenbeek, Hasselt, Ham, Olen, Wijnegem). Positions of ALSs are indicated as blue triangles and catch-release locations (C&R) as grey asterisks.

7.3.2 Tagging procedure

118 Eels were caught in the upstream part of the canal during summer, autumn and winter of two consecutive years (i.e. 2014 and 2015) using double fyke nets, just upstream of the shipping lock complexes in Genk, Diepenbeek and Hasselt. Of those, 70 silver eels were tagged and released on site in the Albert Canal (Fig. 7.1): 13 eels were caught and released in 2014 at Hasselt, five were caught and released in 2014 at Diepenbeek, 27 eels were caught and released in 2014 at Genk. Another 36 eels were caught at Genk in 2015, of which ten were released at that location and the latter 26 were released at one point in canal section D. Several morphometric features were measured in order to determine the eel maturation stage according to Durif et al. (2005): total length (TL, to the nearest mm), body weight (W, to the nearest g), the vertical and horizontal eye diameter (ED_v and ED_h , respectively, to the nearest 0.01 mm) and the length of the pectoral fin (FL, to the nearest 0.01 mm) (Table 7.1). Only females were tagged, since males are smaller than the minimum size handled in this study (< 450 mm (Durif et al., 2005)). Both FIV ($n = 1$) and FV ($n = 69$) silver eels were tagged. Eels were tagged with V13-1L coded acoustic transmitters (13×36 mm, weight in air 11 g, frequency 69 kHz) and V13P-1L coded acoustic transmitters (13×48 mm, weight in air 13 g, frequency 69 kHz) from VEMCO Ltd (Canada) (Table S2). The latter transmitter type has a pressure sensor, but those data were not used in this study. After anaesthetising the eels with 0.3 ml L^{-1} clove oil, tags were implanted according to (Thorstad et al., 2013) and the wound stitched with resorbable polyfilament. Eels recovered in a quarantine reservoir for approximately 1 h and were subsequently released at the first ALS upstream of their catch location or in section D (Fig. 7.1).

Table 7.1: Number of tagged female eels per stage with their different morphometrics: total length (TL), body weight (BW), horizontal and vertical eye diameters (ED_h and ED_v, respectively) and pectoral fin length (FL). Means ± sd and ranges (between brackets) are indicated.

Stage	Number	TL (mm)	BW (g)	ED _h (mm)	ED _v (mm)	FL (mm)
FIV	1	837	1050	10.80	12.49	24.03
FV	69	821 ± 71 (620-957)	1137 ± 306 (522-1970)	10.95 ± 1.01 (9.10-15.00)	10.40 ± 0.89 (8.10-12.13)	40.96 ± 3.94 (31.04-51.60)

7.3.3 Acoustic network

Within the framework of the Belgian LifeWatch observatory, a network of ALSs (VR2W, VR2Tx and VR2AR, VEMCO Ltd, Canada) has been deployed in Belgium and The Netherlands (Fig. S2). These ALSs register the transmitter ID with date and time of the detection. Note that the data of the ALSs not located in the Albert Canal were only used to determine if eels were able to leave the Albert Canal and are therefore not described or discussed here. 23 ALSs were deployed in the Albert Canal itself and another four in the entry of the secondary canals connected to the Albert Canal (Fig. 7.1). In the Albert Canal, ALSs were deployed up- and downstream of every shipping lock (n = 13), near the tidal sluices in Antwerp (n = 3), at the junction with the Schelde-Rijn canal (n = 1), at the junction with the Meuse (n = 2) and evenly spread in section A (n = 4) to cover the sluice complexes of Wezet and Lanaye (Fig. S1). As such, eels were not detected when residing between two ALSs in the same canal section.

However, this set-up was chosen to maximise the probability of detection for migrating eels. The stations were moored at the bank with weights and a small buoy. In this way, the hydrophone was directed upwards in the water column.

7.3.4 Data processing

The 70 tagged silver eels were tracked between 3rd September 2014 and 20th December 2016, resulting in a dataset with 1,541,521 detections. To determine residency times (i.e. the time between arrival and departure at an ALS), residency searches were performed with the VUE software (VEMCO Users Environment, VEMCO Ltd, Canada). This allowed reducing the data by accumulating the number of detections during a fixed period of time. We applied an absence threshold of one hour (i.e. the maximum time permitted between detections within a single residency period) and a detection threshold of one detection (i.e. the minimum number of detections required for a residency period). The residency search resulted in intervals with arrival and departure times per eel at each ALS. Between an arrival and departure within the same detection interval, the number of detections and the residence time were calculated (Verhelst et al., 2018c).

To address the research question about migration success, the entire dataset was used. Research questions about migration speed and temporal behaviour were further subdivided into several specific subquestions (see Sections 7.3.5, 7.3.5, 7.3.5 and Table 7.2) which were addressed using data on the migration period only (in other words, the residence time preceding a migration period was removed). An eel was considered migratory when the previous and next detection intervals were at an ALS preceding and following that ALS in the

migration direction (Verhelst et al., 2018c). For two eels, no migration intervals were obtained, although they were detected in the Meuse. Hence, these two eels were removed from the analysis for research questions related to migration speed and temporal behaviour. Note that all but one of the eels detected in the Meuse were released in canal section A, which has an open connection with the river Meuse, and therefore did not encounter shipping locks in the Albert Canal. Hence, eels detected in the Meuse were not taken into account for the analysis of research questions about migration speed in shipping locks, shipping lock delays and the circadian pattern. All data analyses were performed with the free R software (R Development Core Team 2017) .

Table 7.2: For each research question and subquestion (see Sections 7.3.5, 7.3.5, 7.3.5 and Table 7.2 for a detailed description of the subquestions), a different subset of the data was used (the number of detections and percentage of data relative to the total dataset are given) and the statistical test was chosen accordingly.

Research question	Number of detections	Percentage of total dataset	Statistical test
1 Migration success and routes	1,541,521	100%	None
2 Migration speed and delays			
a. Overall migration speed	326,970	20.1%	One-way Anova with Games-Howell post-hoc test
b. Migration speed canal section	326,970	20.1%	Kruskall-Wallis test with Dunn's-Test
c. Migration speed shipping lock	20,550	1.3%	Kruskall-Wallis test
d. Shipping lock delay	269,567	17.5%	Kruskal-Wallis test
3 Temporal behaviour			
a. Circadian canal section passage pattern	9,768	0.6%	Nested generalized least squares model
b. Monthly travelled distance	276,697	17.9%	Poisson generalized linear mixed model

7.3.5 Data analysis

Migration success

Eels were categorized in four movement classes: eels migrating towards the Schelde Estuary (S-eels) or towards the Meuse (M-eels), potential migrants towards the Schelde Estuary (S_p -eels) and non-migratory eels (NM-eels) (Fig. 7.1). Eels were considered of class S when they were last detected at the ALSs in the Schelde Estuary, while M-eels were last detected in the Meuse (Fig. S2). Eels were classified as S_p if they were successively detected in at least three different canal sections, pointing at a directed movement towards the Schelde Estuary; eels detected in two canal sections or less, were classified as NM-eels. In addition, for the S_p - and NM-eels we checked at which detection station they had last been detected.

Migration speed and delays

To analyse if the migrating eels were delayed, we calculated four metrics: 1) the overall migration speed of the S-, M- and S_p -eels (NM-eels were removed from the statistical analysis) as the time needed to cross the distance between the first and last detection. A one-way ANOVA with Welch correction was performed on log-transformed data, since the variances were not homogenous. Following a significant ANOVA result, a Games-Howell post-hoc test for multiple pairwise comparisons was applied (Games and Howell, 1976).

2) We calculated the migration speed per canal section as the time needed to cross that canal section (i.e. the time of the first detection at the ALS at

the upstream end of a canal section till the last detection at the ALS at the downstream end of the canal section, divided by the distance of that section). We tested if the migration speed differed according to movement class and canal sections (A-G) by applying a nonparametric Kruskal-Wallis test, since assumptions of normality and homogeneity of variances were not met. If the test proved to be significant, a pairwise test for multiple comparisons of mean rank sums (Dunn's-Test) with Bonferroni correction was applied.

3) For S- and S_p -eels we calculated the time needed to cross a shipping lock complex (i.e. the time between the last detection at an ALS upstream of the shipping lock till the first detection at an ALS downstream of the shipping lock). To test if the calculated time differed over the six shipping lock complexes, a non-parametric Kruskal-Wallis test was performed, since the assumptions of normality and homogeneity of variances were not met.

4) We analysed waiting behaviour near the shipping locks for S- and S_p -eels by calculating the residence times at the ALSs up- and downstream of the shipping locks. A non-parametric Kruskal-Wallis test was performed to test if the residence time upstream of the shipping locks differed significantly with the residence time downstream of the locks. If this proved to be significant, we checked if there was a difference in residence time between the ALSs located upstream of the shipping locks by means of a non-parametric Kruskal-Wallis test.

Temporal behaviour

Both seasonal and circadian behaviour patterns were analysed. For the seasonal patterns, we calculated the distance travelled per month (i.e. the dis-

tance between the first and last detection at an ALS for a particular month) for each eel and within each movement class (i.e. S-, M- and S_p -eels). A nested generalized least squares (GLS) model was applied as the variances were not homogenous, and for each movement class we set the month with the highest average distance as the reference level. To help interpreting these results, we calculated the average monthly water flow and water temperatures of section F for 2015 based on data obtained by the Hydrological Information Center (Fig. S3). Note that environmental data was not available for every canal section. However, water flow and temperature did not differ substantially between the canal sections and over the different years (Hydrological Information Center, pers. comm.).

Regarding the circadian pattern, we analysed when eels migrate from one canal section to another. The number of detection records was summed per circadian phase. Consequently, four different circadian phases were determined and linked to each departure in the dataset: dawn (start of civil twilight to sunrise), day (sunrise to sunset), dusk (sunset to end of civil twilight and night (end of civil twilight to start of civil twilight) (Verhelst et al., 2018c). Timestamps of sunset, sunrise and twilight were obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil/index.php>; coordinates: N50°57' E5°20'). To analyse if eels moved between canal sections during the night, a nested (we analysed circadian activity within the different movement classes) Poisson generalised linear mixed model (GLMM) with transmitter ID as random effect was applied. One S_p -eel did not migrate between different canal sections and was therefore not included in the analysis.

7.4 Results

7.4.1 Migration success

In total, 24 eels succeeded to leave the system. Equal numbers of silver eels reached the Schelde Estuary and the Meuse ($n = 12$ in both cases); another 15 eels migrated towards the Schelde but did not leave the system during the study period. The majority of the eels ($n = 31$) were classified as non-migratory (Fig. 7.1). For both the S_p - and NM-eels, approximately one third was last detected at a detection station downstream of a shipping lock. Another third of the S_p -eels was last detected in section G (the docks of Antwerp). Only a minority was last seen at a side canal of the Albert Canal (i.e. canal Dessel-Kwaadmechelen) (one and two eels for the NM- and S_p -eels, respectively).

7.4.2 Migration speed and delays

The mean overall migration speed (i.e. the speed between the first and last detection) differed significantly between the movement classes (Welch ANOVA, $F = 5.809$, $df = 2.000$, $p < 0.05$) (Fig. S4), being approximately three times higher in M-eels (0.054 m s^{-1}) than in S_p -eels (0.018 m s^{-1}) (Games-Howell post-hoc test, $t = 3.393$, $df = 18.5$, $p < 0.05$) and S-eels (0.012 m s^{-1}) ($t = 2.790$, $df = 15.7$, $p = 0.067$), the latter two not differing from each other ($t = 0.956$, $df = 24.9$, $p = 0.611$).

In contrast, the median migration speeds, calculated within the canal sections, differed not significantly between the different movement classes (KW-

test, $\chi^2(2) = 4.1211$, $p = 0.1274$), even though they were threefold higher for S-eels (0.036 m s^{-1}) than for S_p -eels (0.012 m s^{-1}) (Fig. 7.2).

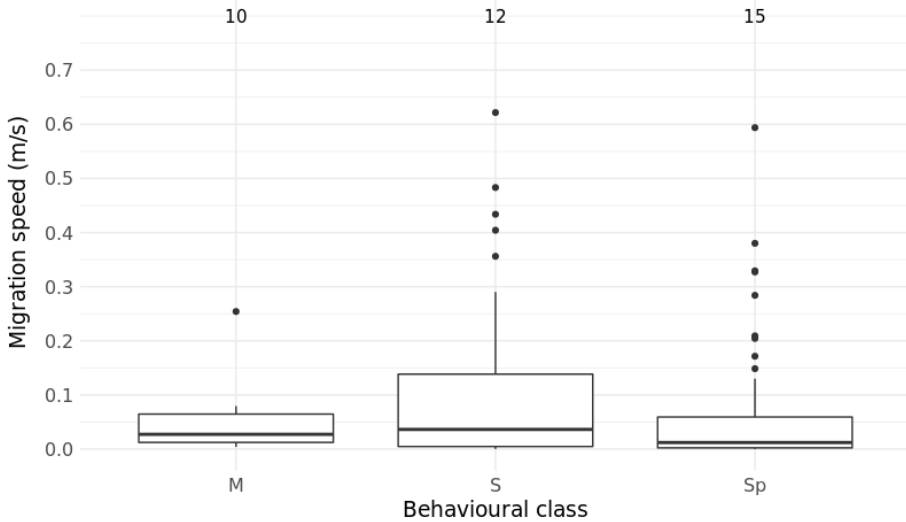


Figure 7.2: The migration speeds, calculated within the canal sections, between the different movement classes (M, S_p and S). The number of eels taken into account for each class is indicated above the boxplots.

Median migration speed differed significantly between canal sections (KW-test, $\chi^2(6) = 15.912$, $p = 0.014$), a difference which could be largely attributed to a significantly higher swimming speed in sections E (0.071 m s^{-1} (range: 0.0007 - 0.6217 m s^{-1})) compared to G (0.002 m s^{-1} (range: 0.0013 - 0.1487 m s^{-1})) (Dunn's Test, $t = 3.54$, $p = 0.0082$) (Fig. 7.3, Table S3). Note that the highest maximum migration speeds were found in section D, E and F (0.5939 m s^{-1} , 0.6217 m s^{-1} and 0.4833 m s^{-1} , respectively).

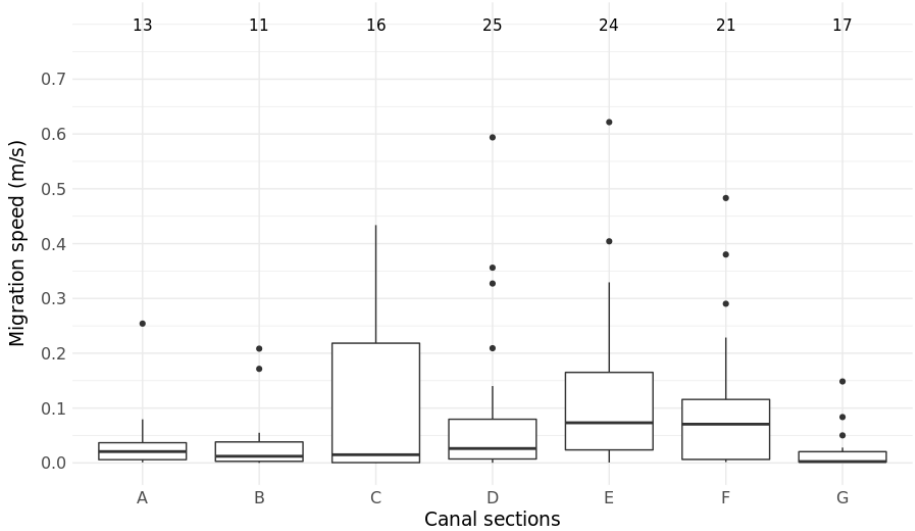


Figure 7.3: The migration speeds per canal section (A-G). Numbers of eels detected in each canal section are indicated above the boxplots.

The median time needed to cross a canal section for S- and S_p -eels was 1.36 h (range: 0.30-435.13 h) and 1.54 h (range: 0.07-671.74 h), respectively, and did not differ significantly between canal sections (KW-test, $\chi^2(5) = 8.9555$, $p > 0.05$ and KW-test, $\chi^2(5) = 10.661$, $p > 0.05$ for S- and S_p -eels, respectively) (Fig. 7.4).

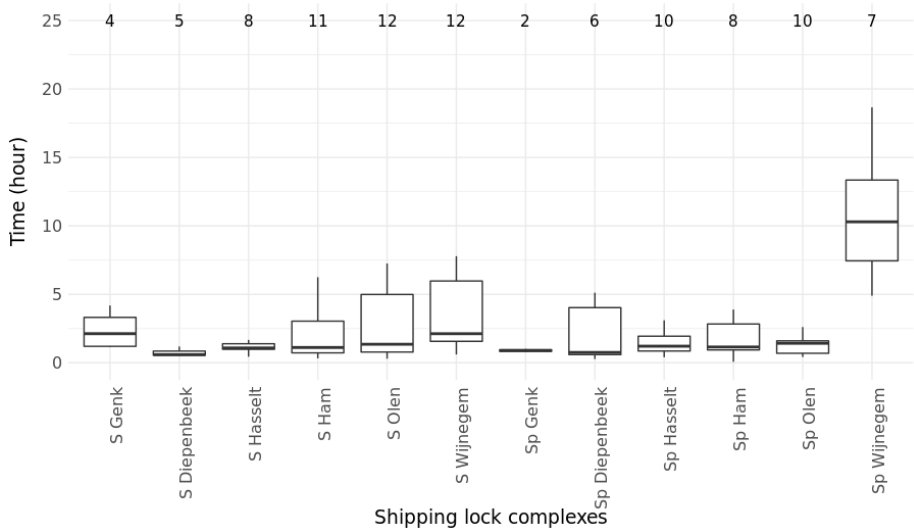


Figure 7.4: The time (in hour) needed to cross the six shipping lock complexes (Genk, Diepenbeek, Hasselt, Ham, Olen, Wijnegem) for S- and S_p -eels. Outliers are not shown in the figure.

The median residence time for S- and S_p -eels was 74 min (range for S-eels: 0.5-13719 min; range for S_p -eels: 0.4-18739 min) and was twice as high up-stream of the shipping locks (KW-test, $\chi^2(1) = 16.328$, $p = 5.328e-5$ and KW-test, $\chi^2(1) = 105.76$, $p < 2.2e-16$, respectively) compared to the downstream located ALSs (Fig. 7.5). No significant differences in median residence time between the different upstream ALSs were found (KW-test, $\chi^2(5) = 7.1454$, $p > 0.05$)

(Fig. S5).

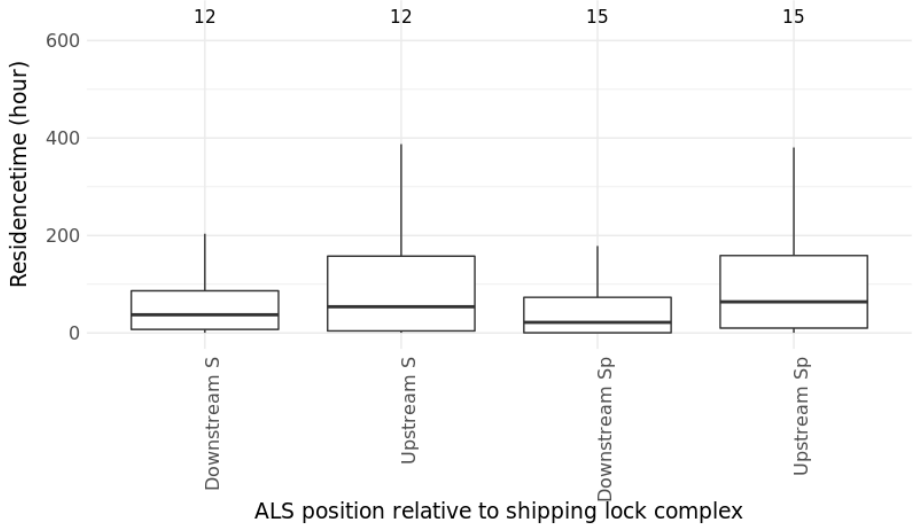


Figure 7.5: Residence times at up- and downstream locations of the shipping locks for S- and S_p -eels. Note that outliers are not shown in the figure.

7.4.3 Temporal behaviour

Temporal patterns in migration distance

In general, all movement classes showed essentially the same monthly pattern with migration distances being significantly longer in autumn and spring (Fig. 7.6) (for model details, see Table S4). Both S- and M-eels covered the largest distances in October (59 km and 22 km, respectively), while S_p -eels travelled the largest distance in November (31 km). High migration distances of all three classes were also found in May and/or June, whereas the lowest migration

distances were found in February (from 2 km for S- and S_p -eels to 8 km for M-eels).

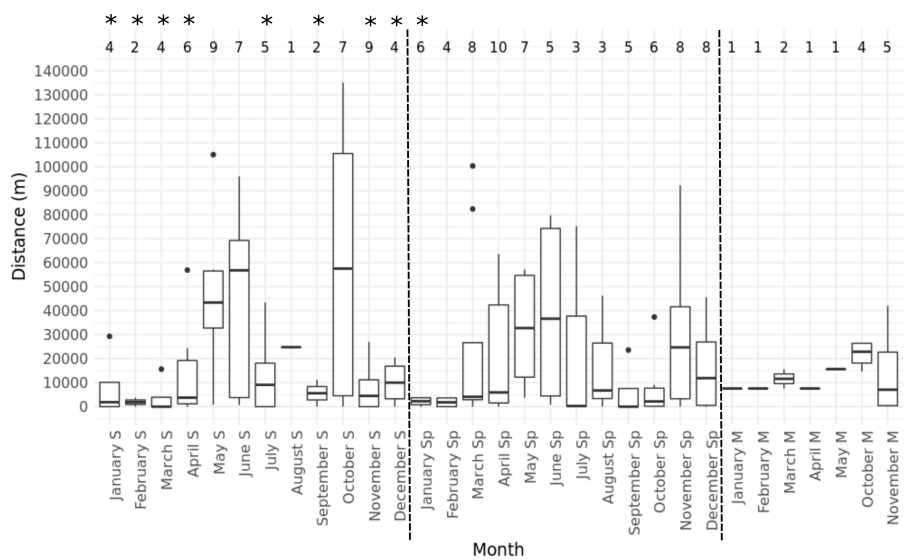


Figure 7.6: The monthly migration distances of the three movement classes (S, M and S_p ; separated by dashed lines). The number of eels detected during each month are indicated above the boxplots. Asterisks indicate a significant difference ($p < 0.05$) with the reference level (i.e. the month with the highest distance). For S- and M- eels, this was October and for S_p -eels November.

Circadian migration patterns of eels in a shipping canal

For both S- and S_p -eels, the majority of the shipping lock complex passages happened during the night (Fig. 7.7), but only for the S_p -eels nocturnal passage was significantly higher than passage during daytime (Poisson GLMM, $z = -$

2.169; $p = 0.03$; for model details, see Table S5).

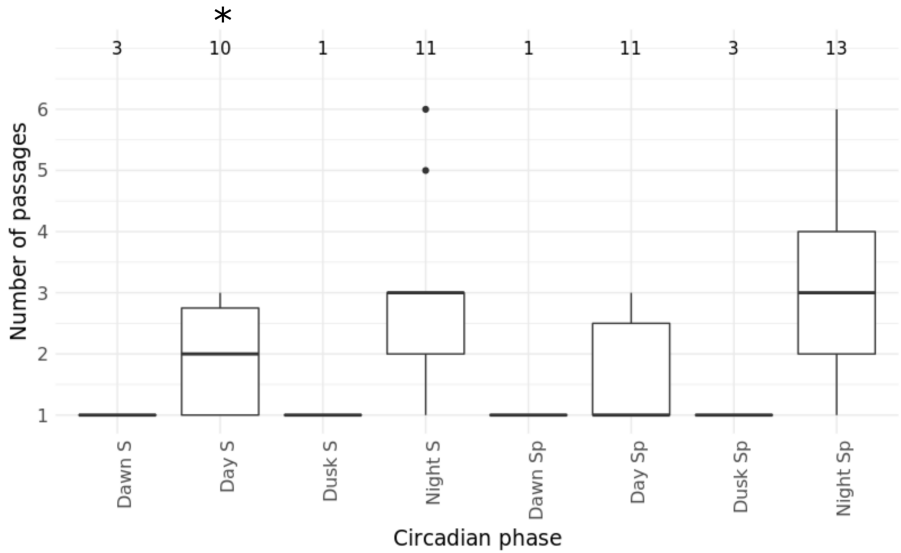


Figure 7.7: The number of shipping lock passages during the four different circadian phases (dawn, day, dusk and night) for the movement classes S and S_p . The number of eels taken into account is indicated above the boxplots. The asterisk indicates a significant difference ($p < 0.05$) between diurnal and nocturnal passages for S-eels.

7.5 Discussion

The eels tracked in our study were classified in four different movement classes (S, M, S_p and NM). Although all tagged eels were considered silver eels (FIV and FV) which should be migrating (Durif et al., 2005), the definition of migrat-

ing eel should be interpreted with care. Specifically, 31 eels did not show a clear migration pattern and were therefore classified as NM-eels. Even if these eels would show migratory behaviour after our study, they will have been delayed substantially. Since some dispersion events may strongly resemble failed migration attempts, eels may have been classified migratory, while they were actually showing long distance dispersion; it is difficult to distinguish between a failed migration event and a dispersion event.

7.5.1 Migration success

During the study period, only 34% of the tagged eels left the Albert Canal while another 21% made attempts, indicating that eels face difficulties when migrating through shipping canals. In the Schelde Estuary, for instance, 71% of FIV and FV silver eels tagged at the upper limit of the estuary reached the lower part of the system. This also indicates that the applied method to classify silver eels and surgery did not affect our results substantially (Verhelst et al. unpublished data). In the Loire Estuary, a large number of silver eels (86%) were detected at the most downstream locations as well (Bultel et al., 2014). Since eels depend on flow direction to migrate from freshwater systems into the marine environment (Travade et al., 2010; Verhelst et al., 2018c; Vøllestad et al., 1986), the low number of successful migrants may be due to the highly regulated water flow of the Albert Canal. Indeed, the operation of the shipping locks causes frequent and irregular changes in flow direction (i.e. a couple of times per hour). Nonetheless, the majority of the migrating eels followed the net flow direction in the canal and moved towards the Schelde Estuary. A smaller part migrated downstream towards the Meuse, but this may be the consequence of

the location where these eels were released: all but one of the M-eels were released in canal section A, which has multiple connections with the River Meuse via the shipping locks in Lanaye and Wizet and the open connection at Monsin. Consequently, eels migrating towards the Meuse encountered fewer or no barriers than S- and S_p -eels, explaining why they were successful in reaching the Meuse. In addition to an irregular water flow and direction, tag expulsion (although normally rare) (Jepsen et al., 2002; Thorstad et al., 2013) and mortality may have been a potential cause of unsuccessful migration of S_p - and NM-eels. Mortality could have occurred as a consequence of predation, fishing or injuries resulting from turbine or sluice passage or ship propellers. Although interference of shipping vessels with the transmitter emissions may be possible, it is difficult to assess because the impact can vary according to the size of the ships and whether they are moving or docked.

The present results are in line with the idea that the silver eel stage is reversible to a semi-yellow stage in freshwater environments when they fail to migrate to the sea (Feunteun et al., 2000; Svedäng and Wickström, 1997). It is unknown what proportion of eels which did not migrate or failed to leave the canal during the study period may still do so in the future. In any case, these eels have been substantially delayed.

7.5.2 Migration speed and delays

The average migration speed of M-eels (0.054 m s^{-1}) was > three times higher than that of S- and S_p -eels (0.012 m s^{-1} and 0.018 m s^{-1} , respectively) and similar to the overall migration speed in a free flowing tidal river (0.052 m s^{-1} (Bultel et al., 2014)). The higher migration speed of the M-eels is likely ex-

plained by the fact that all but one of them were released in the canal section next to the Meuse, leaving them fewer or no barriers to pass compared to the S- and S_p -eels. Moreover, that canal section has multiple routes to the Meuse, among which an open connection at Monsin. Nonetheless, migration speeds for M-, S- and S_p -eels was substantially lower than average migration speeds in other studies conducted in freshwater systems, i.e. 0.30 m s^{-1} - 1.13 m s^{-1} (Breukelaar et al., 2009; Piper et al., 2017; Verbiest et al., 2012). Average migration speeds may be partly misleading, since it may mask large differences in swim speeds between different habitats. (Bultel et al., 2014) observed that eels actually migrate faster when approaching an estuarine environment: their slower migration speed is likely attributed to waiting behaviour in the upper sections of the estuary as the directional speed found in the lower sections was similar to silver eel swim speed in previous studies (i.e. 0.56 m s^{-1}). This contrasts markedly with our results, where migration behaviour was disrupted in the Albert Canal shipping canal: migration speed was low throughout the different canal sections, reaching a minimum in the most downstream section. Since water flow direction in the different sections of the canal changes numerous times per day, we suggest that the slow migration speeds in the canal are likely caused by disorientation due to a lack of a consistent unidirectional water flow. The relatively higher maximum migration speeds in sections D, E and F of the canal may then be explained by the more frequent operation of their respective shipping locks. Specifically, in Ham, Olen and Wijnegem, more ships were transported over those three shipping locks, but note that multiple ships per lock could be transported. In contrast, the slowest migration speed in section G of the Albert Canal can be attributed to the distribution of the water mass over the docks of Antwerp, resulting in a decrease of water flow (Hydro-

logical Information Center, pers. comm.). For their orientation in this section, eels may depend on currents caused by tidal shipping lock operation, which can only be detected in the vicinity of the locks. In this context, it is striking that one third of the S_p -eels reached section G, but were never detected in the Schelde Estuary. It is possible that the dynamic environment of the estuary impairs the detection probability (Reubens et al., 2018), yet 71% of the silver eels tagged in the Schelde Estuary were detected in the lower part (Verhelst et al. unpublished data). A faster and more unidirectional movement towards the sea could be facilitated by the detection of olfactory cues in the estuarine and marine environment (Barbin et al., 1998). As tidal shipping locks (but also non-tidal shipping locks further upstream) prevent the intrusion of marine water and its migration cues for eels, this may also have an impact on the eels' delay and slower swim speeds in shipping canals. Indeed, once inside the Schelde Estuary, S -eels migrated at an average speed of 0.74 m s^{-1} (unpublished data).

Our study also demonstrates that eels were significantly delayed upstream of shipping locks and it took them relatively long to pass these locks. This indicates that the locks may act as a direct migration barrier for downstream migrating eels. Pumping stations and hydropower plants have been reported before as migration barriers for migrating eels (Buysse et al., 2015; Verhelst et al., 2018c; Winter et al., 2006) and several mitigation measures have been proposed (e.g. acoustic fences (Sand et al., 2000), bar racks (Russon et al., 2010), fish friendly adaptations (Hecker and Cook, 2005) and fish passes (Clay, 1994)). Shipping locks have only been reported sporadically as migration barriers for upstream migrating fish (Buysse et al., 2008; Klinge, 1994). Yet, American eels have been shown to use shipping locks to migrate upstream (Verdon and Desrochers, 2003). Our study is therefore the first to demonstrate that they may

also affect downstream fish migration. Weirs, which can be opened during an excess of water, can provide a solution for this problem; however, their efficiency may be very low, as was the case for the Schelde River in Belgium (Buysse et al., 2008). The shipping locks in the Albert Canal don't have weirs. Hence, adequate management measures such as stimulating gravitational flow or fish passes are necessary to facilitate eel migration over shipping locks.

Encountering substantial delays, eels may be more prone to diseases, predation and fishing, and consequently, mortality (Acou et al., 2008; Marmulla, 2001; Sjöberg et al., 2017; Verhelst et al., 2018c). Delays may also cause eels not reaching the spawning grounds on time. Although being an anadromous species, for Sockeye salmon (*Oncorhynchus nerka* Walbaum) it has been shown that spawning success was correlated with the date of arrival (Burnett et al., 2017). Nonetheless, Righton et al. (2016) hypothesized that the eels' migration may be more flexible than thought. Also, it is unknown if obstructed migratory fish encounter an increased state of physiological stress or what the impact may be on the fish' fitness. As such, knowledge on fish migration delays needs further research and is currently insufficient to provide proper management measures (Silva et al., 2017).

7.5.3 Temporal behaviour

Temporal patterns in migration distance

There is scientific consensus that European silver eels generally migrate in autumn, although migration peaks in spring have occasionally been observed (Aarestrup et al., 2008; Sandlund et al., 2017; Verbiest et al., 2012). In this study,

the successful migrants (S- and M-eels) migrated the longest distances in autumn, but substantial large distances were also travelled in spring. S_p -eels even bridged longer distances in spring than autumn. For these S_p -eels, it is plausible that the longer travelled distances during both autumn and spring months are linked with migration behaviour. During spring and autumn, the average water temperature range of the Albert Canal (quantified by a temperature measurement in section F in 2015) was 7.5 °C-17.10 °C and 11.4 °C-18.6 °C, respectively, which is approximately within the temperature window during which Vøllestad et al. (1986) (i.e. 4 °C-18 °C) found the majority of silver eels migrating downstream in the river Imsa, Norway. In addition, although the average monthly water flow was low, peaks were found in May and October. This may have triggered or even guided seaward migration of silver eels in our study. It is unlikely that water flow alone could trigger migration, since another water flow peak in February did not elicit migration, perhaps because the water temperature was too low (i.e. 4.3 °C) (Vøllestad et al., 1986). As such, an interaction between water flow and other triggers like water temperature may be relevant (Buysse et al., 2015). Spring migration, then, might be the result of insufficient migration triggers during the preceding autumn (Westin, 1990), or an insufficient body condition (Aarestrup et al., 2008).

Circadian migration patterns of eels in a shipping canal

Although S- and S_p -eels showed a delayed and potentially disoriented migration behaviour, they still primarily moved from one canal section to the next at night, which is in line with the eel's natural behaviour pattern reported in previous studies (Travade et al., 2010; Vøllestad et al., 1986). The low number of

passages during dusk and dawn may be attributed by the short duration time of those circadian phases. Nocturnal migration is likely a predator-avoidance mechanism in the canal, since turbidity in the canal is low and large numbers of cormorants (*Phalacrocorax carbo* L.) frequently hunt in the area, which have been shown to predate on eels (Ibbotson et al., 2006). This means that although sluices are primarily operated during daytime, eels are likely to pass them at night. Consequently, potential management actions may be most effective at night.

7.5.4 Implications for management

To our knowledge, this study is the first to describe silver eel migration behaviour in a shipping canal (here the Albert Canal). Only a small part of the silver eels was able to leave the Albert Canal during a study period of 27 months and their migration speed was typically very low, probably as a result of the regulated water flow and presence of shipping locks in the canal. This implies that eels may get trapped or be slowed down substantially inside shipping canals, making them more prone to predation and diseases. Hence, heavily regulated shipping canals are most likely an unsuitable migration route for European eel. However, migration through anthropogenic canals may be the best available option if canals can provide a shortcut for migrating eels or if the alternative route is more hazardous (e.g. the Meuse contains several hydropower plants, resulting in substantial mortality rates of silver eels (Verbiest et al., 2012; Winter et al., 2006)). Therefore, we propose several management actions to reduce migration delays. First, an increased gravitational flow in the canal could provide a better cue for eels to find their way downstream. Based on the temporal res-

ults of this study, this measurement may be most effective at night and during spring and autumn. A second option would be to construct fish passes to overcome shipping locks. For instance, it has been shown that eels can make use of undershot sluice gates at small-scale hydropower plants (Egg et al., 2017). However, efficient downstream fish passes are scarce and there is an urgent need for improved knowledge on this issue. The results of the present study also have repercussions for the implementation of stocking of glass eels as part of the eel management plan imposed by the European Eel Regulation (in order to recover the population, the European Union adopted a Council Regulation (European Eel Regulation; EC no. 1100/2007)). For instance, in 2017, 21% (i.e. 18 out of 85 kg) of the glass eels imported in Flanders for seeding purposes were stocked in the Albert Canal. Our study strongly indicates that only 34% of these eels will successfully migrate out of the system and hence potentially contribute to the population. Therefore, unless the passability for eels is improved, we suggest to reduce, or even stop stocking glass eels in large shipping canals and apply stockage in systems where the chances to reach the sea are sufficiently high, such as polder systems which are mainly dewatered via gravitational flow through tidal sluices or via fish friendly pumps.

Chapter 8

Heading south or north: novel insights on European silver eel *Anguilla anguilla* migration in the North Sea

Published as:

Huisman, J.*; Verhelst, P.*; Deneudt, K.; Goethals, P.; Moens, T.; Nagelkerke, L.A.; Nolting, C.; Reubens, J.; Schollema, P.P.; Winter, H.V. 2016. Heading south or north: novel insights on European silver eel *Anguilla anguilla* migration in the North Sea. *Marine Ecology Progress Series* **554**: 257 - 262.

For the supplemental material, we refer to the online version of the article:

<https://doi.org/10.3354/meps11797>

*Joint first authorship

8.1 Abstract

The European eel is a critically endangered fish species that migrates from coastal and freshwater habitats to the Sargasso Sea to spawn. However, the exact migration routes and destination of European eel are still unknown. We are the first to observe southward migrating silver eels in the North Sea. Eels were tagged with acoustic transmitters in 3 different river catchments in Western Europe and swam to the Dutch-Belgian coastal zone during their spawning migration. Therefore, at least part of the Western European population of eels migrates towards the English Channel, in contrast with the Nordic migration route hypothesis. This different migratory route may affect the energy reserve available for spawning and therefore the contribution of these eels to the population. As such, increasing our knowledge of marine eel migrations contributes to the goal of achieving sustainable eel stock management.

8.2 Introduction

The European eel has a complex life cycle, and despite extensive research, many questions still remain unanswered (e.g. what migration routes do they take, how do they orient themselves, what is the mortality rate during the marine migration stage) (Tesch, 1977). Due to technical inabilities to track silver eels, migration routes and migratory behaviour remain largely unknown.

As eels only spawn once and do not feed during migration (Tesch, 1977; Chow et al., 2010), they must rely on their fat reserves for both migration and spawning. It is therefore generally assumed that silver eels take the energetic-

ally most favourable migration route to their spawning grounds (van Ginneken and van den Thillart, 2000). Experts tend to agree on the Nordic migration route hypothesis, which states that European eels from Northern Europe migrate northward in the North Sea, passing the British Isles, after which they reach the Atlantic Ocean (Tesch, 1979) (Fig. 8.1). Acoustic telemetry studies conducted in the German Bight demonstrated that silver eels released at sea swim northwestward (Tesch, 1992; Tesch and Rohlf, 2003). Research in the Baltic yielded similar results, indicating that silver eels migrate in a southwestern direction to exit the Baltic Sea, after which they migrate in a northwestern direction towards Scotland (Westerberg, 1979; Karlsson, 1984). More recently, the Nordic route was confirmed by a study in Sweden using pop-up satellite archival transmitters (PSATs) (Westerberg et al., 2014). Although orientation by an imprinted map is unlikely (Westerberg et al., 2014), the reason for the directional choice of the Nordic migration route is still under debate: the most frequently presented explanations are geomagnetism, flow detection, olfactory orientation and sense of depth (Tesch, 1974).

Despite the plausibility of the Nordic migration route hypothesis, this route has not been confirmed for silver eels migrating from Western European tributaries to the Sargasso Sea. For these eels, an alternative and shorter route would be through the English Channel (the sea between southern England and northern France) (Fig. 8.1). So far, research on marine silver eel migration has been carried out on eels artificially displaced from freshwater environments into the sea (Westerberg et al., 2007; Aarestrup et al., 2009; Béguet-Pon et al., 2015; Wysujack et al., 2015), or mainly focused on deep coastal zones and open oceans, but many migrating silver eels also have to cross large shallow tidal seas. The knowledge gap on migratory routes and behaviour in these systems

deserves further attention, especially in coastal regions, which are often heavily impacted by anthropogenic disturbances.

We explored European silver eel migration by acoustic telemetry in a shallow sea, i.e. the North Sea. Cooperation between separate projects in Belgium, Germany and The Netherlands allowed us to cover a wide geographical range of this species. The results provide novel insights into the marine migration routes and behaviour of European eel, which may contribute to a more efficient conservation of the species; the results also emphasize the importance of international cooperation in order to address these large-scale fish migration issues.

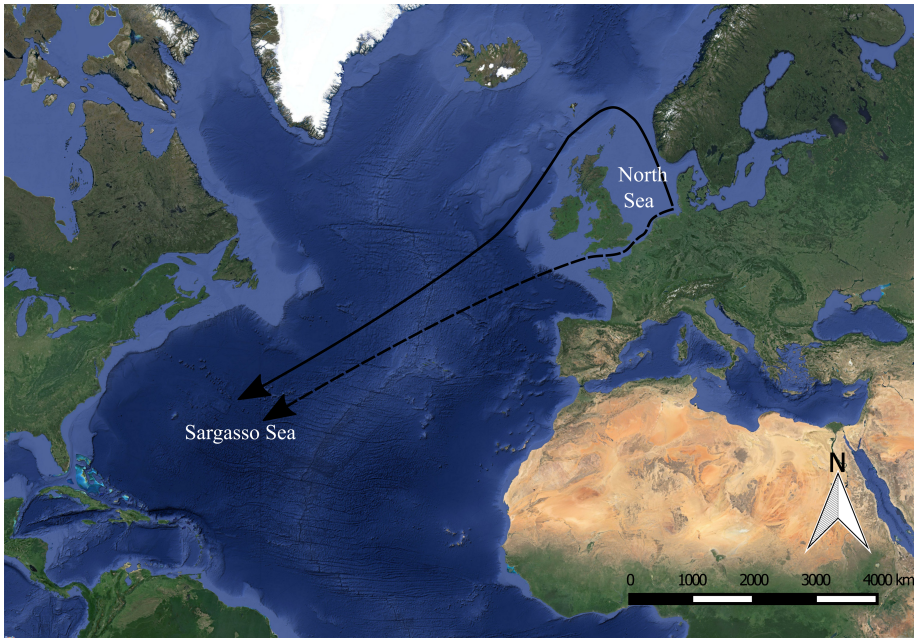


Figure 8.1: Possible silver eel migration routes from western and northeastern Europe. Solid line: Nordic migration route based on Tesch (1979) and Westerberg et al. (2014); dashed line: southwestern migration routes through the English Channel based on the results of the present study.

8.3 Materials and Methods

8.3.1 General methodology

This study was based on detections of tagged eels from the LifeWatch observatory, which installed a permanent acoustic network at the Dutch-Belgian coast

(www.lifewatch.be/en/fish-acoustic-receiver-network)(Fig. 8.2). The detected eels were tagged for other independent projects focusing on eel migration at migration barriers and in altered river systems. The projects used identical acoustic telemetry, which provided the opportunity to investigate marine silver eel migration routes. In 4 different projects, eels were caught in fresh water, tagged and released at their catch location (Fig. 8.2, Table S1). The studies were conducted in 3 different catchments in Western Europe: 2 in the Ems catchment, one in the Schelde catchment and one in the Meuse catchment. Although the aim of the original projects differed, it was the observations at marine detection stations of these tagged eels that were used for this study.

8.3.2 Description of experiments

Within the framework of the LifeWatch observatory, a permanent acoustic network of 54 ALSs (VR2W, VEMCO Ltd, Canada) has been operational since the spring of 2014 in the Schelde Estuary (33 ALSs) and the Belgian part of the North Sea (BPNS) (21 ALSs). The ALSs are moored at strategic locations to maximise the probability of detection (Fig. 8.2): 2 arrays in the Schelde Estuary to detect incoming and outgoing fish, and a scattered pattern in the BPNS (since it is impossible to cover the whole area). The network in the BPNS focuses on the nearshore region, as most of the eels were expected there. ALSs were moored at navigational buoys with stainless steel chains ca. 4 m long, weighing ca. 17.5 kg. ALSs were attached to the chain with stainless steel clamping rings, with the hydrophone directed downwards (Fig. S1).

As stated previously, in this study we used information from a number of independent experiments in which eels were tagged. In the summer of 2012,

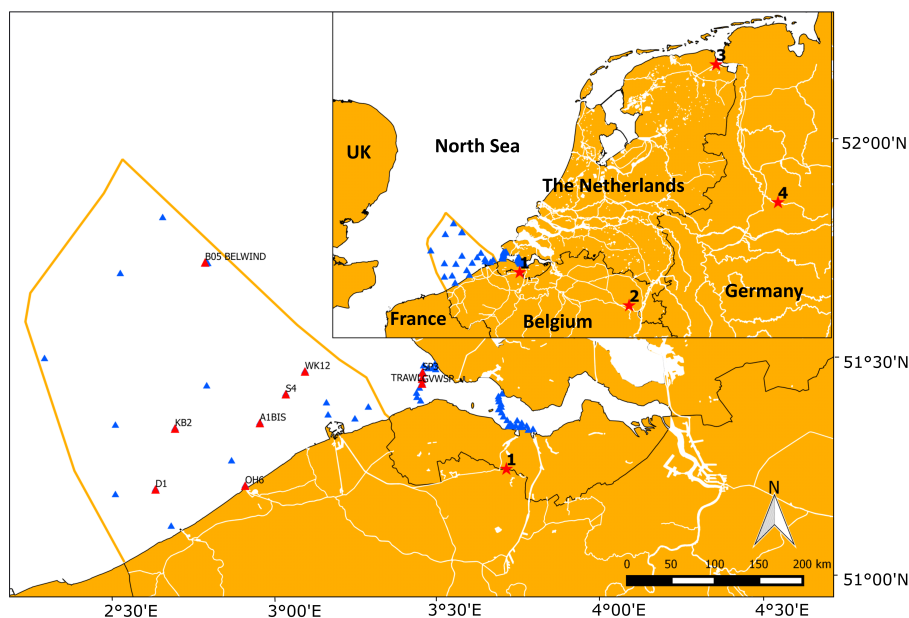


Figure 8.2: LifeWatch acoustic telemetry network in the Schelde Estuary and Belgian part of the North Sea. The triangles are acoustic listening stations deployed on marine buoys. Eels were detected at red triangles, of which the buoy name is given. Asterisks indicate release locations of the tagged eels: (1) Boekhoude (Zwartesluisbeek, Schelde catchment); (2) Genk (Albert Canal, Meuse catchment); (3) Delfzijl (Ems Canal, Ems catchment); (4) Einen (Ems River, Ems catchment).

we tagged 73 eels at a polder area in Boekhoude (Schelde catchment, Belgium) to investigate the effect of a pumping station on silver eel mortality and behaviour during downstream migration (Buyse et al., 2015). In 2013 and 2014, we tagged a total of 60 eels at the Albert Canal in Genk (Meuse catchment, Belgium) to investigate silver eel migration in relation to sluices and anthro-

pogenically influenced hydrology. In December 2014, we caught 185 eels in the Ems river near Emden (Ems catchment, Germany) and upon tagging, we translocated these eels approximately 250 km upstream to Einen to compare migratory behaviour of silver eels in the Western German Canal System versus that in the River Ems. In autumn 2014, we tagged 40 eels at a polder area in Delfzijl (Ems catchment, The Netherlands) to explore silver eel migratory behaviour and investigate the efficiency of an intertidal fish pass at a pumping station. To determine the maturation stage of all tagged eels according to Durif et al. (2005), total length (to the nearest mm), body weight (to the nearest g), average eye diameter (to the nearest mm) and length of the pectoral fin (to the nearest mm) were measured (Table 8.1). Silver eels were tagged with coded acoustic transmitters (V9 and V13, VEMCO Ltd, Canada) following Baras and Jeandrain (1998) and released at their catch location, except for the 185 eels caught near Emden (see above). Additional information about the tags and methods of capture can be found in Table S1 in the Supplement.

Detection time of individual eels at an ALS was related to sunrise, sunset and tides. Sunrise and sunset data were obtained from the Astronomical Applications Department of the US Naval Observatory (<http://aa.usno.navy.mil/index.php>). Modelled tidal data were obtained from the Royal Belgian Institute of Natural Sciences, Operational Direction Natural Environment (KBIN-OD Nature).

Table 8.1: Tag ID, body weight (BW), total length (TL), pectoral fin length (FL), horizontal and vertical eye diameter (ED_h and ED_v, respectively), release date (dd/mm/yyyy) and life stage of detected eels, and release location and catchment within the specific water body. Stage FIII is the transition stage between yellow and silver; Stage FIV is the stage at which eels begin their downstream movement and stop growing; Stage FV is the migrating stage (Durif et al., 2005).

Tag ID	BW (g)	TL (mm)	FL (mm)	ED _h	ED _v	Release date	Stage	Release location
17773	1011	770	33.97	9.57	10.06	15/01/2015*	FIV	Einen, Ems catchment (Ems River)
19433	510	665	35.00	8.00	9.00	22/10/2014	FV	Delfzijl, Ems catchment (Ems Canal)
19437	948	790	41.00	9.00	9.00	22/10/2014	FIII	Delfzijl, Ems catchment (Ems Canal)
19439	513	650	35.00	11.00	9.00	22/10/2014	FIV	Delfzijl, Ems catchment (Ems Canal)
19442	641	725	35.00	8.00	8.00	22/10/2014	FIII	Delfzijl, Ems catchment (Ems Canal)
19450	853	790	37.00	9.00	9.00	30/10/2014	FV	Delfzijl, Ems catchment (Ems Canal)
19459	599	690	38.00	8.00	8.00	30/10/2014	FV	Delfzijl, Ems catchment (Ems Canal)
26488	1088	772	40.76	9.63	10.45	14/10/2014	FV	Genk, Meuse catchment (Albert Canal)
26491	920	770	36.00	10.00	10.00	15/10/2014	FV	Genk, Meuse catchment (Albert Canal)
28261	1229	789	34.85	10.80	10.00	18/10/2013	FV	Genk, Meuse catchment (Albert Canal)
31877	663	712	38.60	10.80	10.00	17/07/2012	FV	Boekhoute, Schelde catchment (Zwarteluisbeek)

*Eel ID 17773 was the only translocated eel, and thus not immediately released upon catching and tagging. It was caught on 28/12/2014 near Emden (Ems River), tagged on 08/01/2015 and released on 15/01/2015 in Einen (Ems River), ca. 250 km upstream.

8.4 Results and discussion

8.4.1 Migratory routes and activity

Between 25 October 2014 and 17 October 2015, 11 eels were detected at the marine acoustic network; 7 originating from the Ems catchment (6 from The Netherlands and 1 from Germany), 3 from the Meuse catchment (Belgium) and 1 from the Schelde catchment (Belgium) (Fig. 8.2, Table 8.1). Of the 40 eels tagged in the polder area at Delfzijl (The Netherlands), 30 migrated successfully to sea as they were detected at an ALS on the seaside of the pumping station. Of these 30 eels, 6 (20%) were detected at the Dutch-Belgian coast and hence migrated southwards. In the Albert Canal (Belgium), 3 of the 60 eels migrated to sea and all 3 were detected (100%). Of the 73 eels tagged in the polder area at Boekhoude (Belgium), 2 migrated to sea, 1 of which (50%) was detected at the marine acoustic network. Although 93 of the 185 tagged eels in Einen (Germany) reached the North Sea, only one ($\leq 1\%$) was detected in the BPNS. The reason can only be speculated, but it is possible that some of these eels took the Nordic migration route (Westerberg et al., 2014) or resided in the Ems until conditions became more favourable to proceed their migration. Migratory eels have indeed been observed to undergo a resident stage in the lower part of rivers and estuaries (Aarestrup et al., 2008). Given the vast area of the North Sea, these detection rates are high and indicate a route that may well be chosen by a larger part of the eel population.

Our results are the first to show a southwest oriented migration route of silver eels emigrating from 3 different Western European catchments, head-

ing to the English Channel in order to exit the North Sea on their way to the Sargasso Sea. This is in contrast with the Nordic migration route hypothesis, and demonstrates that at least some of the Western European eels take another route. Moreover, we present results on eels that were tagged in freshwater and released on-site, in contrast to previous studies (Tesch, 1974, 1979, 1992; Aarestrup et al., 2009; Wysujack et al., 2015) in which eels were translocated from freshwater habitats to the sea. It is not clear if translocation affects eel behaviour, but allowing them to emigrate naturally avoids this potential bias.

Eels were only detected from mid-October until early February; no detections were obtained between March and October 2015. Ten eels were detected less than 20 km offshore, whereas only one was approximately 50 km offshore. It should be noted that 15 out of 21 ALSs in the BPNS are located within 30 km offshore, which could explain why the majority of eels was detected within this zone. Ten eels were detected at single ALSs only, but all of them at different locations in the BPNS. These eels were each detected less than 10 times by an ALS and always within a single hour, indicating that they were migrating through the detection field without residing there for longer periods. Only 1 eel was detected by 4 different ALSs, 3 of which were located at the mouth of the Schelde Estuary and one in the BPNS.

8.4.2 Swim speed

Marine migration speed was calculated for the 6 eels from Delfzijl, 1 eel from Boekhoude and 1 eel from Genk that migrated via the Schelde Estuary since these eels were detected at the channel mouths at sea (Table S2). The other 2 eels from Genk and one from Einen were not detected at the river mouths,

since no ALSs were present in that area. As migration behaviour in freshwater and the marine environment might differ considerably (e.g. retention periods resulting in an overestimation of swim speed), the swim speeds of the latter 3 eels will not be discussed. We found a mean (\pm SD) swim speed of 20 ± 4.5 km d⁻¹ (range: 12 to 25 km d⁻¹) for the eels from Delfzijl and 24 km d⁻¹ for the eel from Boekhoude. Such swim speeds are in accordance with Westerberg et al. (2014). The eel from Genk migrated at a speed of only 1 km d⁻¹, which is probably due to a retention period in the Schelde Estuary (Aarestrup et al., 2008).

8.4.3 Diurnal activity and flow-related migration patterns

Seven eels were detected at night, 3 during daytime and 1 eel was detected during both day and night. This is roughly in accordance with the general assumption that eels migrate at night to avoid predators (Westerberg et al., 2007). However, a recent study documented eel migration during both day and night (Wysujack et al., 2015). Moreover, diurnal migratory behaviour in the North Sea may also be affected by high turbidity.

The tidal action in the North Sea results in a change of flow direction twice per day. As such, the southward ebb tidal flow is directed towards the English Channel twice per day, whereas the net residual flow over the tides is directed northwards. The majority of the eels (73%) were detected during a southward tidal flow (Table S2). This suggests that eels selectively use tidal flow in the North Sea to migrate in an energetically favourable way, a behaviour known as selective tidal stream transport: a fish ascends into the water column when the transporting tide is in the preferred direction and descends to the bottom to

maintain its position in the opposing tidal current. Selective tidal stream transport has been documented for both the European eel (McCleave and Arnold, 1999) and the American eel (Parker and McCleave, 1997; Béguer-Pon et al., 2014). The application of PSATs in further research could provide more insight into this issue.

8.5 Conclusions

Our results provide strong evidence that at least part of the Western European population of silver eels migrate southwestward in the North Sea and use the English Channel as a migration route. Moreover, we have shown that at least some eels from different catchments in Belgium, Germany and The Netherlands use this migration route. Our results also suggest that eels are predominantly active at night and selectively use tidal flow to migrate. This study highlights that acoustic telemetry is an effective technique to track eels over large distances, and in coastal marine environments. However, to answer questions about the migratory behaviour of European eel in the Atlantic Ocean, other techniques such as PSATs may be better suited. Further research on migration routes and behaviour could help resolve the question of how many of the silver eels escaping to sea actually reach the spawning ground and effectively contribute to recruitment. Furthermore, different migration routes may have different bio-energetic implications: some routes may be energetically more demanding, leaving less energy for spawning. As such, management might need to focus more on areas where eels take an energetically favourable route and contribute more to spawning. However, we do not have enough information

yet to determine whether something significant is happening during marine migration and whether the inland management actions taken are effective. To further clarify migration behaviour of diadromous fish in the marine phase, transnational cooperation and investment in large-scale marine detection arrays (which enable the study of migration routes and behaviour) are needed, and could be instrumental in the conservation of diadromous fish species in general, and European eel in particular.

Chapter 9

General discussion

9.1 Main findings from this dissertation

Yellow eels are rather sedentary with a strong site fidelity and limited home range. Previous research indicated that the ranging behaviour of yellow eels varied between 285 m and 5,060 m (Baras et al., 1998; McGovern and McCarthy, 1992; Thibault et al., 2007; Walker et al., 2014). However, large scale movements, such as upstream migration, have been reported (Feunteun et al., 2003). Our results confirmed this, as the average movement range of the tracked yellow eels in the polder area were 3,917 m with the eels having a strong site fidelity as well, but five of the 56 tagged eels showed a movement range between 10 and 20 km (Verhelst et al., 2018d). We could not find any relationship between environmental variables and movement range, which we attribute to the opportunistic feeding behaviour of yellow eels (Lammens et al., 1985; Schulze

et al., 2004; Van Liefferinge et al., 2012). Opportunistic feeding behaviour challenges the existence of disruptive selection, hypothesising that the dichotomous and strongly deterministic characterization into 'broad' and 'narrow' headed eels is erroneous. Indeed, in Chapter 4 we found no proof for disruptive selection, since the head width distribution of 272 eels caught at the weir in Merelbeke had a unimodal head width distribution. Even more, the relative condition increased from narrower headed eels to broader headed eels. Consequently, eels could indeed not be divided in two distinct head-width groups. Instead, their head widths showed a continuum of narrow to broad.

Related to silver eel migration behaviour, in Chapter 5 we illustrated strong evidence that silver eels apply STST in the Schelde Estuary and therefore it is likely that the tides help eels to migrate in a bioenergetically efficient way through estuaries. Also, applying STST suggests eels can make a distinction between ebbing and flooding tide, indicating that cues other than currents play a role in orientation.

Silver eel tracking in a polder and shipping canal obstructed with migration barriers such as weirs, pumping stations, tidal sluices and shipping locks, revealed substantial delays, slow migration speeds and even migration arrests (Verhelst et al., 2018a,c). Consequently, these barriers negatively affect the eel population as delayed eels are more prone to disease and predation. Also, the effect of delays on the fish's fitness is currently unknown and therefore requires further research (Silva et al., 2018).

Finally, the observation that at least part of the silver European eels migrate through the English Channel to exit the North Sea emphasized the importance of large scale international networks to track migratory species over admin-

istrative borders. It also holds important implications for management. Different migration routes may have different bio-energetic implications: some routes may be energetically more demanding, leaving less energy for spawning. As such, management might need to focus more on areas where eels take an energetically favourable route and contribute more to spawning (Huisman et al., 2016) (see Section 9.3.4).

9.2 Eel management revisited

9.2.1 Migration barriers

River continuity is a necessity for fish migration and in particular for diadromous species. Of the 250 diadromous species (Myers, 1949), many have historical low numbers (Limburg and Waldman, 2009). Likely, various factors contributed to their decline, but migration barriers have been considered to be one of the main causes (Limburg and Waldman, 2009). As stated in the introduction, migration barriers prevent both the upstream migration of glass eels, elvers and yellow eels as the downstream migration of silver eels (Drouineau et al., 2018b; Feunteun, 2002; Moriarty and Dekker, 1997). Considering the critical status of the European eel population, effective management to allow safe passage is urgently needed. Various measures are taken to allow the ingress of glass eels into freshwater habitats near coastal areas, such as eel ladders and tidal barrier management (Mouton et al., 2011b; Legault et al., 1990; Benecke, 1884). Yet, to increase the eel abundance further upstream, restocking is the main applied management measure, the efficiency of which is doubtful (see

Section 1.5.2).

Different types of barriers exist such as large barrages, flood-control dams, flood gates, weirs, hydropower stations, shipping locks, tidal sluices, pumping stations and fisheries (Bruijs and Durif, 2009). In this dissertation, we investigated the effect of shipping locks and pumping stations on silver eel migration. Yet, since hydropower stations have a similar effect on silver eels as pumping stations, we will discuss solutions for them as well.

Pumping and hydropower stations

Due to climate change, the associated rising sea level and a growing human population, pressure on dewatering systems is likely to intensify in the future, resulting in the instalment of more pumping stations and hydropower turbines (Beatty et al., 2014; Hannah et al., 2007; Hermoso and Clavero, 2011; Maceda-Veiga, 2013). Pumping and hydropower stations cause severe mortality among downstream migrating silver eels. Propeller pumps, for instance, can kill up to 97% of migrating silver eels, while this is near 20% for Archimedes pumps (Buysse et al., 2014, 2015). For turbine stations, among which Kaplan turbines are the most used turbine type in Europe, mortality ranged from 20% to 38% (Hadderingh and Bruijs, 2002; Winter et al., 2007). Note that a river can have multiple hydropower stations, leading to an accumulated silver eel mortality rate along a river stretch.

Despite their severe impact and although the EU Eel Regulation is in place for almost ten years, effective management measures are still lacking. Considering pumping stations, fish-friendly screw-adaptations have been made, but proved ineffective (Buysse et al., 2015). Eel racks (Russon et al., 2010)

and light deflection systems (Hadderingh et al., 1992, 1999) are applied to prevent eels from migrating through hydropower turbines, yet with varying results (Bruijs and Durif, 2009). Solutions enabling safe passage of downstream migrating silver eels through pumping and hydropower stations can act on different fronts. First, development of fish-friendly screws is a pressing issue, as in many cases it is the only possible migration route, especially for pumping stations in polders (Fig. 9.1). In those systems, the water level is below sea level, making gravitational discharge, for instance via fish passes, impossible (see further). The exact cause of damage and subsequent mortality is well known: fish get struck by the first winding of the screw or get stuck/-crushed between the winding of the screw and the inner side of the housing of the screw. Yet, success stories with zero mortality through adapted screws are rare. Even more, in some cases no difference in silver eel mortality was found before and after fish-friendly adaptations to an Archimedes pumping station in a polder in Flanders (Buysse et al., 2015). Related to turbine stations, supposed fish-friendly improvements have been developed over the classic Francis, Kaplan and Archimedes turbines. These include low pressure turbines (<http://fishflowinnovations.nl>), fish-friendly Archimedes turbines (<http://fishflowinnovations.nl>), Alden turbines (Silva et al., 2018), Kaplan turbines with 'Minimum Gap Runner' (MGR) technology (<http://www.voith.com>), DIVE turbines (<http://www.dive-turbine.de>) and Very Low Head (VLH) turbines (<http://www.vlh-turbine.com>). Yet, further testing in the field is required and hence, development of fish-friendly adaptations requires further research and bringing together behavioural ecologists and engineers are necessary to lead to effective solutions. Second, development of downstream fish passes can be a promising management measure to aid silver eel migration.

Fish passes have been successfully applied for upstream migrating fish, as fish can be attracted to an attraction flow of a fish pass near a migration barrier (Bunt et al., 2012; Roscoe and Hinch, 2010; Silva et al., 2018). However, downstream migrating fish follow the main current, making them less prone to attraction flows near the margins of the main river. Consequently, development of fish passes to aid downstream migrating fish is not straightforward, as the main current runs through pumping and hydropower stations. Even more, in case of pumping stations in polders, water is pumped from watersheds with a low water level to a high water level. This leads to a fish pass with water running back into the watershed with the lowest water level, resulting in an incoming attraction flow which is in conflict with silver eels following the downstream current (Buysse et al., 2015). Yet, the delays and exploration behaviour upstream a migration barrier accompanied with deflecting behaviour by eel- and trash-racks may open opportunities to guide eels towards the inlet of a downstream fish pass, especially near turbine stations (Bruijs and Durif, 2009; Gosset et al., 2005; Silva et al., 2018; Verhelst et al., 2018c). Gosset et al. (2005) observed that 56% - 64% of the downstream migrating eels used flap gates located near the end of a trash-rack instead of migrating through a small hydropower station, while the flap gates had a discharge of only 2% - 5% of the turbine discharge. Further, Egg et al. (2017) observed silver eels migrating through an undershot sluice instead of the provided eel pass at a small hydropower station in Germany of which eel migration through the turbines was prevented by an eel rack. In conclusion, due to the lower water level than the sea in polders, the only probable eel migration route is often via the pumping station. Consequently, fish-friendly screw improvements are urgently needed. In case of turbine stations, development of undershot sluice gates or flap gates

could aid downstream fish migration when applied next to the trash- and eel-racks of turbine stations (Fig. 9.1). They would even be more efficient when the turbine station is shut off during migration periods, leading to the main current running via the undershot sluice gate or flap gates (see Section 9.2.3).

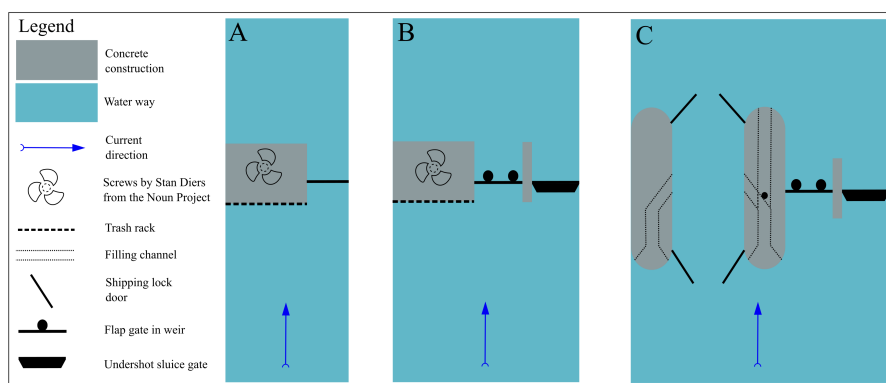


Figure 9.1: Proposed adaptations to enhance safe downstream fish passage at a pumping station in a polder (A), turbine station (B) and a shipping lock complex (C).

Shipping locks

In contrast to pumping and hydropower stations, a direct mortality effect on migrating silver eels has not been shown for shipping locks and tidal sluices (but see Section 9.3.2). Yet, they cause substantial delays, making eels more prone to diseases and predation (Verhelst et al., 2018a). In general, there are three ways to help eels overcome shipping locks: (1) via opening of the lock gates, (2) via channels which transport water from the river/canal into the shipping locks for filling (note that not all shipping locks have these channels)

or (3) via specifically designed fish passage systems. The substantial delays upstream the shipping locks in the Albert Canal indicated that eels had difficulties to overcome the shipping locks (Verhelst et al., 2018a). Consequently, it is likely that the attraction flow generated by opening a shipping lock or filling channel may be insufficient to attract eels (Buysse et al., 2008) or that the filling of shipping locks comes with high levels of turbulence and underwater noise, which may deter eels (Piper et al., 2015; Sand et al., 2000). Therefore, aiding eel passage over shipping locks requires a higher attractiveness of the eels to the shipping locks or passage systems and development of fish-friendly water inlets and filling channels. For example, widening the filling channels may make them prone for eels to find them and move unharmed with a lower (i.e. less turbulent) filling flow (Fig. 9.1). In addition, channels with as few bends as possible, may reduce eel strikes against the channel walls. If it is impossible to widen or straighten the channels, reducing the filling discharge may allow eels to pass safely. Yet, in this case attractiveness is likely to be reduced, but eel deflection systems towards the inlet may help.

Similar to the fish passes near hydropower stations, management could opt to develop undershot sluice gates or specialised passes next to shipping locks to allow silver eel passage. However, flap gates could be integrated in the shipping lock filling channels, with one part of the channel made inaccessible for eels and diverting to the shipping lock for filling, while the other part functions as a corridor to transport the eels to the other side of the shipping lock (Fig. 9.1).

9.2.2 Regulated water flow

Apart from migration barriers, an important feature for efficient migration is the water flow. Various studies observed that silver eel migration is linked with an increase in discharge (Bultel et al., 2014; Travade et al., 2010; Vøllestad et al., 1986). Consequently, a reduction or disruption in natural flow may affect silver eel migration. Indeed, in the studied polder, for instance, eel migration came to a standstill in the Braakman. This was likely caused by the infrequent dewatering of the Braakman: it was only dewatered when the water level of the Schelde Estuary was lower than the Braakman. The resulting water flow however was probably too marginal for the eels to detect and consequently leave the system (Verhelst et al., 2018c).

In the Albert Canal and the Zeeschelde, the tracked migratory eels ($n = 70$ and $n = 58$ respectively) showed substantial different migration successes. Of the 70 tracked silver eels in the Albert Canal, only 12 reached Antwerp (i.e. the most downstream part of the canal near the estuary) during a 27 month study period; another 15 were still migrating towards Antwerp while 35 were considered not showing migration behaviour at all (the remaining 12 eels migrated to the Meuse) (Verhelst et al., 2018a). In contrast, 52 of the 58 migrating eels from the Zeeschelde reached Antwerp within three months. The migration speed between the two groups which reached Antwerp was different as well: the 12 Albert Canal eels migrated on average at 0.01 m s^{-1} (notably, the 15 eels still migrating towards Antwerp migrated at a similar average speed of 0.02 m s^{-1}), while the 52 eels in the Zeeschelde migrated five times as fast (i.e. 0.05 m s^{-1}) (Verhelst et al., 2018b). Yet, the latter eels applied STST and migrated during ebbing tide at an average speed of 0.92 m s^{-1} . Even more, further down-

stream the estuary (i.e. the Westerschelde), eels speeded up substantially (0.42 m s^{-1}), yet with a comparable speed during ebb as in the Zeeschelde (0.95 m s^{-1}). This indicated that eels are less reluctant in their migration behaviour as they descent an estuary. In contrast, the lowest average migration speed for the Albert Canal eels was found at the most downstream section in Antwerp (0.02 m s^{-1} ; in the other sections the speed ranged from $0.06 - 0.18 \text{ m s}^{-1}$, except for the most upstream section (0.003 m s^{-1})). The slower speeds of the Albert Canal eels are probably not only attributed to migration obstruction by the shipping locks, but also to the inconsistent and bidirectional regulated water flow, a.o. due to shipping lock operation resulting in back-and-forth moving waterfronts and turbine operation. Even more, the lowest speeds in the most downstream canal section are likely attributed to a standstill in water flow: the already low water flow distributes over the large area of the docks.

Consequently, to aid silver eel migration, a more consistent downstream flow needs to be generated. In polders, pumping stations are activated when a specific water level threshold is achieved. During heavy rainfall, pumps could be activated over long, uninterrupted periods, creating a consistent, unidirectional flow. Yet, to stimulate pumping over longer periods and consequently silver eel migration, water managers could opt to allow water levels to rise at a higher level or drain a polder until a lower level, if it is raining sufficiently to bring the polder back at its minimum water level. Obviously, in accordance with the agriculture sector and without flooding risks for inhabitants.

However, in highly regulated shipping canals like the Albert Canal, creating a consistent, unidirectional current poses a bigger challenge. A more consistent, unidirectional flow could be achieved by feeding the canal with a

higher proportion of the Meuse discharge. A first plausible solution may be the construction of weirs next to the shipping lock complexes which can allow water passage next to the shipping locks to generate a more unidirectional flow. However, due to economic interests and lack of space, the construction of weirs is not always feasible. Second, a higher discharge could be generated during specific migration windows (see Section 9.2.3). The shipping locks of the Albert Canal operate from Monday morning 6 a.m. till Saturday evening 10 p.m, and remain closed/inactive on Sundays and holidays. Also, due to limitations of nocturnal navigation, the locks mainly operate during daytime. Eels, in their turn, mainly migrate at night and during autumn (Verhelst et al., 2018a). As such, management could opt to increase the discharge running through the Albert Canal via either (slightly) opened shipping locks, undershot sluice gates or constructed weirs at night during, for instance, October, November and December. In addition, to stimulate a unidirectional flow in the lowest canal section (i.e. the docks of Antwerp), a minimum number of tidal sluices to prevent flooding could be opened during the aforementioned migration windows when the water level of the Schelde Estuary is lower than the Albert Canal to stimulate gravitational flow. Acknowledging that the 'Grensmaas' (i.e. the part of the Meuse bordering Belgium and The Netherlands) needs at least a discharge of $10 \text{ m}^3 \text{ s}^{-1}$ (Anonymous, 2002), water supply is unlikely to be the limiting factor as eels migrate during periods of high precipitation and consequently a higher discharge (Stein et al., 2015; Travade et al., 2010).

9.2.3 Migration windows

To make the above mentioned suggestions more effective or since some can only be applied during a restricted time period (i.e. due to economic importance, water scarcity...), it is beneficial to implement them during specific migration windows. Silver eel migration in Western Europe occurs between August and January, mostly at night and during moments of high precipitation and accompanied discharge (Tesch, 2003; Travade et al., 2010; Vøllestad et al., 1986). Consequently, management could strive to apply measures during those specific moments, leading to, for instance, relative more water through undershot sluice gates or flap gates (Egg et al., 2017; Gosset et al., 2005). Notably, management should act within a region (e.g. Western Europe, Northern Europe...) or even within catchments as there are differences in timing of migration between regions (i.e. eels start to migrate in summer in Northern Europe, but in autumn in Western Europe (Durif and Elie, 2008; Haraldstad et al., 1985; Vøllestad et al., 1986)). Obviously, the spatial resolution on which management should act, depends on the knowledge of the managed catchment and could require further research for actions to be effective. This also holds true for the temporal resolution: telemetry data reveals high resolution spatio-temporal data on silver eel migration and allows for a detailed analysis on the migration routes and environmental triggers. Fitting these data into mechanistic models (e.g. individual based models) could result in interesting management tools (Baetens et al., 2013), narrowing down the spatio-temporal migration windows on which management has to act in order to restore the European eel population. Specifically, such tools could allow the prediction of silver eel escapement, aiding water managers on their decision when mitiga-

tion measures need to be taken. Through the collection of more qualitative and quantitative data, the models will become more accurate and even may take into account biotic factors such as species interactions instead of solely abiotic factors.

9.2.4 Individual variability

An important added value of telemetry, is the tracking of individuals, leading to datasets of individual behaviour. Nonetheless, this poses challenges for data analysis (e.g. autocorrelation) and translating the results to a (sub)population level. The latter is especially important since nowadays management often works on a (sub)population level or in some occasions at life stage levels (e.g. adjusted tidal barrier management to improve glass eel colonisation (Mouton et al., 2011b)). This individual variability translates itself to pronounced variability in movement behaviour, such as migration and swim speed, degree of exploratory behaviour, temporal movement variability, route choice... Obviously some might be at least partly intrinsically determined by the eels morphology; larger eels swim faster than smaller eels (Bainbridge, 1958). Yet, many aspects may depend on the eel's 'choice'.

Anthropogenic interference with the animal kingdom results in selection of specific genotypes, leading to the accompanied phenotype. A well-known example is fisheries-induced smaller size at maturity of fish (Law, 2000). Genotype selection may also occur at freshwater obstructions or even fish passes trying to allow free fish movement. In the polder and Albert Canal, substantial individual variability was observed between silver eels approaching a migration barrier (i.e. pumping station, tidal barriers and shipping locks): some eels

were much more reluctant to pass a barrier than others. Although the effect of delays is not well understood (see Section 9.3.3), delayed eels may have a smaller chance to contribute to the spawning population by an increased susceptibility to disease, mortality or a lower fitness. Yet, their more reluctant movement behaviour and accompanied lower migration speed, may be compensated by a higher fertility. Therefore, migration obstructions may have important repercussions to the genetic diversity of the spawning population. The same holds true for possible management measures to make barriers passable, for instance fish passes. Dependent on the construction of fish passes, they may select for strong swimmers, which may not necessarily coincide with high fertility. Although the effect on the genetic diversity of fish populations of migration barriers and management measures to overcome them is still unknown, from a precautionary perspective, we should take as much individuals as possible into account for management. Telemetry data gives researchers insight in the individual behaviour of animals, allowing a more detailed understanding of how species behave. As such, this may help push management further than (sub)population level and start considering measures on an individual level.

9.3 Remaining knowledge gaps

9.3.1 Methodological constraints

Life stage classification

When eels prepare for migration, they turn from yellow into silver eels (Tesch, 2003). The morphological appearance of silver eels is characterised by a vis-

ible lateral line, large, melanised pectoral fins, dark dorsal side, silver-white ventral side and large eyes. Due to the large eyes, the far end of the mouth does not reach beyond the eyes, which is the case for yellow eels. Hence, classifying silver eels based on the aforementioned external characteristics may be subjective. Consequently, we applied a more objective approach by measuring morphometrics (i.e. total length (to the nearest mm), weight (to the nearest g), horizontal and vertical left eye diameter (to the nearest 0.01 mm) and pectoral fin length (to the nearest 0.01 mm) to deduce the maturation stage according to Durif et al. (2005). This method is widely applied in European eel research (Barry et al., 2016a; Bultel et al., 2014; Simon et al., 2012; Stein et al., 2015). Nonetheless we do acknowledge that the method is not 100% conclusive. For example in the Schelde Estuary, six of the 51 (12%) tagged premigratory staged eels (FIII) migrated upon tagging, while another seven (14%) migrated at the following season upon tagging and 38 (74%) eels did not show migration behaviour at all. In contrast, 13 (62%) of the 21 tagged FIV eels migrated upon tagging, with an additional two (10%) a year later (six eels (29%) did not show migration behaviour). For FV eels, even 25 (86%) of 28 eels migrated upon tagging with a single eel (4%) the year after (three eels (11%) did not show migration behaviour). This variability can be attributed to factors other than the migration classification (i.e. morphometric measurement errors, post-handling stress, unfavourable environmental variables, mortality, tag expulsion...). However, since eels were not obstructed in the Schelde Estuary, it is unlikely caused by delays due to migration barriers. On the other hand, these results may point to a revision of the classification method or at least further fine tuning of the FIII-stage. Nonetheless, due to the low number of FIII eels migrating upon tagging, we suggest not to tag that life stage for silver eel

migration studies of less than a year, but preferentially tag FV eels.

Migration behaviour identification

Animal migration is considered a persistent and unidirectional movement, characterized by the temporary inhibition of station keeping responses such as foraging, territorial behaviour and commuting (Kennedy, 1985). Yet, eel migration is often found to be not continuous (Béguer-Pon et al., 2014; Durif et al., 2006, 2002; Stein et al., 2015). This discontinuous migration behaviour can be explained by various reasons such as the absence of required environmental conditions, STST for migration in tidal environments or even trial runs to test their body condition before they leave for the Sargasso Sea (Hain, 1975). Nonetheless, such discontinuous behaviour makes it hard to distinguish between dispersion/ranging events and possible migration events. This difficulty becomes more apparent in systems where migration is obstructed due to migration barriers or regulated water flows: it is hard to distinguish between ranging and a failed migration event. Nonetheless, yellow eels are highly sedentary with a limited home range (285 – 18,248 m) (Baras et al., 1998; Thibault et al., 2007; Verhelst et al., 2018d; Walker et al., 2014), yet, larger scale explorative behaviour may occur (e.g. in their search for wintering habitat (Hammond and Welsh, 2009)). However, not many studies make a distinction between resident and migratory behaviour (Stein et al., 2015), but consider eels in the migratory silver stage based on external morphology (e.g. Aarestrup et al. (2010); Béguer-Pon et al. (2014); Bultel et al. (2014); Davidsen et al. (2011); Piper et al. (2017); Verbiest et al. (2012)). Consequently, the whole dataset is considered migratory silver eel behaviour. In order to identify migration, three different methods

were tested in this dissertation: (1) progression speed, (2) the method of Lavielle (Lavielle, 1999, 2005) and (3) the triplet method.

Progression speeds can be used as a tool to distinguish between residency and migration behaviour, but require a thorough knowledge of the animal of interest (e.g. range distances during the non-migratory life stage and movement speeds) to justify threshold values. Both yellow and silver eels have been studied extensively leading to sufficient literature to support our applied thresholds (Verhelst et al., 2018b). Yet, this method can only be applied at study sites larger than the range distance of the animal during its non-migratory life stage. In addition, aquatic systems with migration barriers delay eels, leading to biased progression speeds and, consequently, inapplicability of this method. Therefore, we applied this method in the Schelde Estuary only, which is free of migration barriers.

Another possible method to delineate migration is via residence times. The method of Lavielle partitions a trajectory in K segments based on homogeneous mean residence times (Lavielle, 1999, 2005; Barraquand and Benhamou, 2008). Since we were interested to distinguish the eels' trajectories into residency and migration, each individual trajectory was split in two segments ($K = 2$). An acknowledged disadvantage of the method is that it is developed for Lagrangian data which have a constant time interval between detections, while acoustic telemetry data has an Eulerian structure (i.e. a moving object passes detection stations) (Merki and Laube, 2012). Consequently, residency times can only be deduced at detection stations and can lead to misclassifying the tipping point of residency into migration behaviour. Nonetheless, we tested the method in a polder area as it is (1) independent of the biased migration

speed due to the present migration barriers in the system and (2) the polder is located relatively close to the marine environment, challenging the minimum distance threshold to distinguish eel migration from ranging (Verhelst et al., 2018c,d).

A third approach was using the set-up of the network: when a fish consequently passes three ALSs, it is considered migratory; a method similar to the approach by Stein et al. (2015) (an eel was considered migratory if it was sequentially detected at two downstream located ALSs). Since acoustic telemetry networks often have an irregular set-up (i.e. the interdistance between ALSs is not constant), fish residing in parts of the network with a higher density of ALSs may be more easily classified as migrants. Nonetheless, when a constant interdistance between the ALSs is applied, this method may be promising to distinguish between resident and migratory behaviour. The reason why this method was still applied in the Albert Canal was due to the large detection ranges (> 1 km), leading to unreliable residence times at ALSs. Also, due to the shipping locks and heavily regulated water flow, migration was much slower than in previously reported studies tackling silver eel progression, making it difficult to apply a method based on progression speed (Verhelst et al., 2018a).

9.3.2 Physical effect of shipping locks

Despite substantial research during the last few decades on Anguillid eels, especially the European eel, many knowledge gaps remain. A lot of attention regarding eel migration focused on pumping and hydropower stations. However, it is still unknown if shipping locks cause physical damage to eels as well. This physical damage is likely dependent on the mechanical structure

and functioning of the shipping lock, especially during filling and emptying. For instance, openings above water can lead to eels smashing on the water surface or even concrete bottoms of the receiving reservoir, leading to possible damage. Obviously, this problem is less prominent when openings are under water. Another possible problem to overcome shipping locks, are the filling channels. Not only may the eels encounter shear stresses when moving through these channels at the high speed of water transport, they may be subjected to substantial changes in pressure, leading to barotrauma. The latter has been observed for salmonids passing pumping stations and hydropower stations (Brown et al., 2014). Finally, the transported ships themselves may cause damage to fish as well, via, for instance, propeller strikes (Brown and Murphy, 2010). If future research would indicate physical damage on fish during movement in or through a shipping lock, the development of these structures need to be revisited to make them fish friendly, if we want to protect our fish populations.

9.3.3 Effect of delays

Another important knowledge gap, is the effect of delays, caused by migration barriers, on the eel's life cycle (Silva et al., 2018). We can assume that a longer residence in a specific area comes hand in hand with a higher chance of disease, predation and consequently mortality. However, since gonads mature during their migration, delays may lead to a mismatch in gonad maturation and arrival at the spawning grounds. Yet, eels may be able to regulate their gonad maturation via diel vertical migrations in the Atlantic Ocean by ascending to shallower, warmer water at night and diving to deeper, colder water during daytime (Aarestrup et al., 2009). Even more, eels may be flexible in their migration strategy as they could adopt a fast migration and arrive at the spawning event following their onset of migration or arrive a year later at the next event (i.e. mixed migration hypothesis) (Righton et al., 2016). Indeed, although migration generally takes place in autumn in Western Europe (Durif and Elie, 2008), spring migrants are often observed in heavy anthropogenically regulated systems (Acou et al., 2008; Deelder, 1954; Feunteun et al., 2000).

Migration delays can even lead to eels postponing their spawning migration and turning from the silver stage back into a so called semiyellow stage (Svedäng and Wickström, 1997). As gonads start to mature prior migration (Durif et al., 2005), postponing their migration comes with a certain cost: either the eels resorb their gonads or they maintain them for the next migration attempt. It is not known what the effect of this cost is on the migration behaviour or the quality of the eggs and sperm and consequently reproductive success. Investigating the gonads and condition of eels caught at both barrier free systems and heavily regulated systems or even ponds and lakes may shed light on

this knowledge gap. Nonetheless, the relative condition of the silver eels (FV) in this dissertation did not differ between the polder, estuary and canal (Fig. S1), but a more thorough analysis (i.e. fat content, liver weight, pollutants...) may reveal a different result.

9.3.4 Spawning and movement behaviour in the marine environment

Although stated in numerous studies that European eels spawn in the Sargasso Sea, there is still no proof that eels effectively spawn in that area, as spawning has never been observed in the wild, nor have eggs. In addition, the migration routes to the presumed spawning ground are largely unknown as well. However, technological improvements related to telemetry allowed recent discoveries such as the tracking of eels from continental Europe till the Azores (Righton et al., 2016), the first evidence of European eels migrating through the Gibraltar Strait to leave the Mediterranean (Amilhat et al., 2016) and the finding of both a Nordic and Southern migration route to exit the North Sea (Huisman et al., 2016; Westerberg et al., 2014). Locating and sampling spawning eels in the wild would answer important questions related to anthropogenic impacts on the eel population and conducted management. Acknowledging that the eel is a panmictic species (Als et al., 2011), they show a remarkable adaptive capacity to various habitats, which is probably the result of genetic polymorphism (Drouineau et al., 2014; Mateo et al., 2017). Hence, it may be possible to deduce where the spawning eels' growing regions were located, allowing to map the geographical regions which contain the majority of the eels contributing to spawning. Next to growing habitats, different migration routes

may have different bio-energetic implications: some routes may be energetically more demanding, leaving less energy for spawning (Huisman et al., 2016). As such, management might need to focus more on those areas where eels with a substantial contribution to the spawning population depart from or take an energetically favourable route. It also holds true the other way around: when spawning eels from specific regions are only marginally contributing to the spawning stock, the reason could be sought for and, if necessary, management could be improved.

Despite eels show a high phenotypic plasticity in habitat use, behavioural movement studies are mainly conducted in freshwater systems (Acou et al., 2008; Piper et al., 2015; Vøllestad et al., 1986; Winter et al., 2006). Yet, a part of the European eel population is oceanodromous and resides in marine and estuarine environments and lagoons during the growing stage (Tsukamoto and Nakai, 1998). This knowledge gap is especially important since the recruitment decline is based on glass eels migrating upstream, neglecting the oceanodromous part of the population. Consequently, the 90 – 99% decline may be an overestimation.

A large knowledge gap persists in the movement biology of yellow eels in marine and estuarine environments, with only a handful of studies been conducted (Daverat et al., 2006; Walker et al., 2014). Daverat et al. (2006) found that a large part of the eels is resident in marine and estuarine environments, but moved into freshwater systems at least once during their life. However, this tendency decreased with latitude, which is in accordance with the hypothesis that catadromous behaviour is a response to tropical, productive rivers, while anadromy is more common at high latitudes (Gross et al., 1988). It is suggested

that mainly glass eels with a lower body condition adopt an oceanodromous life stage, as upstream migration requires more energy (Edeline et al., 2006). Yet, predation and intra-specific competition is lower in temperate freshwater systems (Ibbotson et al., 2002; Jonsson and Jonsson, 1993), leading to a trade-off between oceanodromy and catadromy.

To partly cover the knowledge gap about yellow eel behaviour in estuarine systems, an acoustic telemetry network of 15 ALSs was deployed from July 2016 till August 2017 in the Drowned Land of Saeftinghe, a saltmarsh area part of the Westerschelde. However, after four weeks of fishing with fyke nets in July – August 2016, only one eel (FII, Total length = 570 mm, Weight = 401 g) was caught and subsequently tagged with a V13 coded tag (VEMCO Ltd, Canada). Upon tagging, the eel moved downstream to the edge of the Drowned Land of Saeftinghe with the main channel of the Westerschelde to subsequently move upstream in the saltmarsh area. Unfortunately, tracking stopped after 16 days at that upstream location (Verhelst et al. unpubl. data). Although the fate of the eel remains speculative, it illustrates that saltmarshes may be used by at least some eels as growing areas. In particular, these systems are full of macroinvertebrates and juvenile fish, which are potential prey for eels (Tesch, 2003). Yet, although it is assumed that eel densities are high in estuaries to population diffusion processes, leading mainly to males (Krueger and Oliveira, 1999), we could only catch a single yellow, female eel. The reason for this remains unclear and different possible explanations may hold true: (i) it could be that a better water quality of the Zeeschelde stimulates eels to migrate further upstream (Guelinckx et al., 2008), (ii) the system is too dynamic to hold many eels (i.e. at low water, only the largest ditches and some deep pools contain water), (iii) competition with shore crab (*Carcinus maenas* L.) is

too high (they proved to be highly abundant during the sampling campaign), despite eels eat crabs (Tesch, 2003) or (iv) our fishing methodology was not sufficient or intensive enough. As a result, the study left more research questions than it solved, emphasising the knowledge gaps of marine and estuarine eel behaviour.

Development in marine/estuarine and freshwater habitats may have certain consequences. For instance, growth rate is higher in estuaries at lower latitudes due to a higher productivity and temperature (Fernández-Delgado et al., 2006). Also, eel sex differentiation is mainly attributed to density, with male eels developing when density is high (Krueger and Oliveira, 1999). Consequently, due to the higher density of eels in estuaries and coastal areas (which in itself is the result of population diffusion processes), these areas may lead to the production of a higher proportion of male eels compared to freshwater systems. Even more, recent research suggests that eels may be genetically determined to be either oceanodromous or catadromous (Stacey et al., 2015).

Due to the marine biological knowledge gap, we have limited understanding about the impact of coastal and estuarine anthropogenic activities, such as migration barriers (both physical and chemical), harbours and coastal protection on oceanodromous eels as well. For instance, prevention of freshwater habitat colonisation may increase the proportion of oceanodromous eels (Clavero and Hermoso, 2015), leading to shifts in growth rate, sexual differentiation and perhaps mortality (e.g. via mismatch between genotype and phenotype). However, historical and current abundance and distribution data of eels is scarce or even non-existent, making it difficult to elucidate changes in population dynamics of oceanodromous eels. Nonetheless, water quality im-

provement in the Schelde Estuary is likely the driver of a larger number of yellow eels being caught upstream the estuary (Guelinckx et al., 2008). On the other hand, coastal and estuarine anthropogenic effects may lead to habitat loss and, consequently, a reduction in the number of oceanodromous eels (Drouineau et al., 2018b). Specifically, development of harbours and coastal fortification has reduced the number of estuaries and lagoons substantially (Gros and Prouzet, 2014; Simenstad and Cordell, 2000). Further, it has been stated that pollution accumulation in catadromous eels restrains successful spawning migration (Belpaire et al., 2016), yet pollution at coastal and estuarine harbours may be substantial (Deschutter et al., 2017) and affecting oceanodromous eels as well.

9.4 Future considerations

9.4.1 International networks

Telemetry allows tracking of mobile species over large spatio-temporal scales, even over administrative borders. Development of international networks not only enhances this large-scale tracking, it encourages cooperation over administrative borders and is consequently beneficial for wildlife management (Lennox et al., 2017). Recently, several local aquatic tracking networks, created by individual research groups, have been clustered in large-scale tracking networks allowing the tagged animals of different researchers and different projects to be detected on a larger scale and consequently expanding the study area substantially. Examples of such networks are the Integrated

Marine Observing System (IMOS, Australia), Atlantic Cooperative Telemetry (North America), California Fish Tracking Consortium, Florida Acoustic Cooperative Telemetry (North America) and the Acoustic Tracking Array Platform (South Africa). Many of these networks are on their turn clustered within the global Ocean Tracking Network (OTN). Recently, the European Tracking Network (ETN) was created to unite the different networks in Europe as well (<http://www.lifewatch.be/etn>) (Section 2.3). Further, not only the physical network is an important feature. It is likely that telemetry will play a more prominent role to meet management goals in the near future (Lennox et al., 2017). Creating large-scale networks stimulates cooperation and discussion, and as such, knowledge exchange between researchers of different institutes will be key for future management.

Clustering local tracking networks into large-scale, administrative border-crossing networks allows a better understanding of animal movement behaviour and has recently led to novel insights (Brodie et al., 2018; Huisman et al., 2016; Sequeira et al., 2018). Expanding these physical and social networks will undoubtedly aid future insights in fish migration and lead management towards sustainable and viable populations.

9.4.2 Open source policies

A prerequisite of (international) cooperation between institutes requires open source policies, so animals can be tracked beyond the local tracking network. Currently, some telemetry companies hold patents on their specific hardware and settings, leading to incompatibilities between telemetry equipment of different companies and as a result to less detections and knowledge. Striving for

open source technology allows a larger flexibility of the applied technology in the large-scale network or even combine different techniques of different companies. Even more, supply and demand, as well as competition between companies may lead to faster technological improvements such as smaller transmitters or lower prices, which in their turn result in tagging more individuals of smaller species or life stages.

In parallel with the technological improvements of telemetry are the development of analytical tools and algorithms. Telemetry researchers all over the world face similar problems at different steps of the data analysis: formatting the data, visualisations and data exploration, data analysis... Not only does this require an increasing collaboration between biologists, computer scientists and statisticians, making developed code reusable and publically available will enhance the scientific community substantially (Lennox et al., 2017). Some developments are already ongoing, such as the VTrack (<https://cran.r-project.org/web/packages/VTrack/index.html>) and glatos (<https://gitlab.oceantrack.org/GreatLakes/glatos>) R-packages of which the former is on CRAN (the Comprehensive R Archive Network) and the latter on gitlab. Both packages contain functionalities and algorithms for acoustic telemetry data assimilation, visualisation and analysis. Note that this development does not need to be limited to the telemetry community, but can be picked up by researchers in other fields of interest as well. Nowadays, different platforms exist to make code publically available (e.g. GitHub Inc., Gitlab). Even more, digital object identifiers can be added to the code, so they can be tracked or even added to a published article. And if you want the code to be picked up even faster, you can write a package for it and put it in an open library of the program it was written for (e.g. CRAN). Consequently, users are able to down-

load and use your code and functionalities.

Finally, making the data publically available can aid science and management as analyses can be conducted on data over vaster regions or longer time spans, leading to more well-found management decisions. An open policy can benefit other end users as well, for example scientists conducting research on global scale distribution patterns of many species (Bosch et al., 2018). Such platforms already exist, for example the Ocean Biogeographic Information System (OBIS) and the Global Biodiversity Information Facility (GBIF). Since the number of telemetry studies is increasing and leads to high resolution spatio-temporal distribution patterns (Hussey et al., 2015), these data are an added value for open species distribution platforms.

However, we should be careful with open data policies as well. Making data publically available allows unprecedented disturbance by people who benefit from the tagged species (Cooke et al., 2017). This can be recreational and commercial fishermen, divers and wildlife photographers, but poachers as well, leading to the opposite effect of conservation. It is therefore crucial to overthink in what form telemetry data can be made publically available (e.g. lowering the spatio-temporal resolution of the detection) and for who (e.g. people registering at a specific website, scientists, policy makers...).

9.4.3 Linking environmental and biological data

The application of telemetry to track aquatic animals dates back to the 70s (Arnold and Dewar, 2001), yet, complex algorithms and models for data analysis have been lagging behind. It is only during the last decade that substantial

improvements have been made on that frontier (Béguer-Pon et al., 2014; Jacoby et al., 2012; Jacoby and Freeman, 2016; Ledee et al., 2015; Pauwels et al., 2014). Nonetheless, many of those studies analyse metrics derived from the movement itself (e.g. arrivals and residence times at ALSs, effect of morphometrics on the movement behaviour, migration speeds and distances...) (Béguer-Pon et al., 2014; Ledee et al., 2015). To analyse effects of the environment on the spatio-temporal animal movement behaviour is not a trivial thing to do, since it requires qualitative and quantitative environmental data and complex algorithms to link those data to telemetry datasets. All the more since the resolution of telemetry data mostly exceeds the resolution of the monitored environmental data (Bruneel et al., 2018). Indeed, many aquatic systems have only one to a handful of environmental data monitoring stations, while telemetry networks often exceed in tens of deployed ALSs over a wide geographical area of the aquatic system of interest (see Chapter 5 and 6). Different solutions for future considerations exist, from the addition of extra environmental sensors in the study area, over the application of transmitters combined with sensors, to the interpolation of environmental variables between different detection stations (Bruneel et al., 2018). Yet, some aquatic systems are currently extensively monitored and the environmental data gaps are filled with interpolation techniques (e.g. the Delft3D model of the Schelde Estuary). It would be of substantial added value to link telemetry data with those systems in the future, not only to improve our insight in animal behaviour, but also to get a more thorough understanding of the impact of system changes to those animals.

This approach could actually be taken a step further. Apart from environmental variables, species interactions can play a significant role in animals' distributions and movements (Verhelst et al., 2016). Many waterways are mon-

itored for macro-invertebrates and fish to assess the water quality (Breine et al., 2004, 2007; Gabriels et al., 2010). Linking these biotic and environmental data to telemetry data may reveal important insights in ecosystem functioning. Even more, it is likely that a higher number of species and individuals will be tracked in the future, leading to more data and more solid models. As such, telemetry will play a more prominent role in efficient management and environmental policy studies (Lennox et al., 2017; McGowan et al., 2017).

9.5 Future recommendations

9.5.1 Management recommendations

To aid conservation and recovery of European eel stocks, the European Union adopted a Council Regulation (European Eel Regulation; EC no. 1100/2007) which imposes a management system that ensures 40% escapement of the spawning stock biomass, defined as the best estimate of the theoretical escapement rate if the stock were completely free of anthropogenic influences. Not only is it unknown if this theoretical rate suffices to save the eel population, per country or catchment, it implies understanding (1) of the annual silver eel production and (2) the annual silver eel escapement. Obviously, these aspects are hard to identify, challenging the evaluation of the European Eel Regulation.

Although many knowledge gaps remain, substantial research has been conducted since the establishment of the European Eel Regulation, leading to various studies emphasising the importance of global change on the European eel population (Drouineau et al., 2018b), such as the impact of ocean climate

change (Miller et al., 2015), pollution (Belpaire et al., 2016), movement barriers (Buysse et al., 2014; Verhelst et al., 2018a,c), introduction of non-native parasites (Palstra et al., 2007) and overexploitation (Aarestrup et al., 2010; Dekker, 2018; Moriarty and Dekker, 1997). With the upcoming evaluation of the regulation, additional research is likely to follow (e.g. towards development of downstream fish passes, fine tune migration models, effect of migration delays...), yet, sufficient knowledge is available to take new steps in eel management.

Despite the numerous factors contributing to the European eel decline, the two main management measures taken are fishing limitations and glass eel stocking. Nonetheless, as long as no adequate actions are taken to reduce mortality related to other factors such as habitat loss and movement barriers, climate change, pollution and the effect of non-native parasites, the aforementioned management measures are unlikely to have a substantial effect (Drouineau et al., 2018b). Glass eel stocking, for instance, may only be beneficial at locations with a minimum of migration barriers near the sea. Nonetheless, genetic research is urgently needed to deduce if glass eel relocation is effective, since recent research indicated that the phenotype or phenotypic plasticity may be determined by the genotype (Stacey et al., 2015).

The results of this dissertation clearly illustrate that downstream migrating silver eels are severely impacted by migration barriers such as weirs, pumping stations, tidal sluices and shipping locks. Although more research is needed to understand the effects of delayed migration on reproductive success (Silva et al. 2018), delayed fish are more prone to diseases and predation, indicating the negative effect of migration barriers. Yet, the results showed opportunities for management to improve silver eel escapement during so called "migration

windows". Specifically, silver eels in Belgium primarily migrated at night during autumn under increased discharge conditions, likely a consequence of increased precipitation (Verhelst et al., 2018a,c). At some locations, it may be feasible to temporarily open migration barriers to stimulate a unidirectional flow and consequently silver eel escapement during those environmental conditions during which silver eel migration is most likely to occur. Further, at other locations alternative migration routes may be stimulated by slightly changing the hydrology of the system, allowing eels to take a safer route by, for instance, avoiding passage through pumping stations or hydropower turbines (Verhelst et al., 2018a,c). In case of the Albert Canal, this would imply that it can act as a short cut for eels growing in the upper reaches of the Meuse River and take the canal as an alternative route instead of the longer Meuse with hydropower stations.

However, these actions come with certain costs (e.g. reduction in hydropower, less shipping, higher water levels in polder areas...), so it may not be straightforward to implement the suggested measures. Hence, ecologists and engineers need to work together to strive for win-win situations between both ecology and economy. Obviously, not only the eel population will benefit from taken measures, but other diadromous and potamodromous species as well.

9.5.2 Research recommendations

The European eel has a complex life cycle with fundamental biological questions still being unanswered. Thus far, the exact marine migration routes of silver eels to the spawning grounds have not been elucidated. Yet, recent technological improvement allowed tracking of silver eels until the Azores

(Righton et al., 2016). Mapping these routes and understanding the accompanying behaviour can teach us how Anguillid eels handle their available bio-energy budgets for successful spawning. For instance, Righton et al. (2016) hypothesised that the migration routes at sea may take 1.5 years before reaching the spawning grounds, which has important bio-energetic repercussions considering the species ceases feeding at this life stage (Chow et al., 2010). As stated in Chapter 8, different migration routes may require different energy demands and consequently, contribution to the spawning stock may not be equal for all eels from various locations in Europe. Therefore, management may need to be tailored according to the energy requirements of the escaping population. For instance, yellow eel growing in areas holding a substantial part of the spawning population may require extra attention. However, more information related to the energy requirements for spawning migration is needed. Further, tracking silver eels until the spawning area could not only reveal anthropogenic bottlenecks at sea, but also migratory problems occurring at sea due to anthropogenic influences during the continental phase (e.g. effects of pollution, the non-native swim bladder parasite *Anguillicoloides crassus* and delays near migration barriers on efficient spawning migration and consequently successful spawning). Also, various studies tracking silver eels at sea observed predation by marine mammals, sharks and tunas (Béguier-Pon et al., 2012; Righton et al., 2016). Although a high predation rate may be attributed to the tagging effect, it may also hold true that migrating silver eels serve as an important food source for many marine predators. Silver eel migration is an annual recurring event over a large spatial scale. Consequently, a substantial reduction in silver eels may have important consequences for large marine predator population dynamics.

Another important scientific field which contributes to the many biological enigmas of Anguillid eels is genetic research. Genetic research has improved substantially over the last decades and this trend will likely continue in the near future. Hence, eel research will benefit from this as well. Specifically, although the European eel population is considered panmictic (Als et al., 2011), genetic patchiness among recruits has been observed (Pujolar et al., 2006). Even more, recent genetic research found evidence against panmixia for the Japanese eel (Igarashi et al., 2018). Hence, further elucidating the genetic structure of Anguillid eels could help determine the effective spawning stock (Pujolar et al., 2006). It also may be possible in the future to determine the different growing locations of the spawning stock, enabling a quantification of migrating eels from different continental regions. In light of this genetic patchiness, future research could unravel if glass eels have different genetic adaptations. Specifically, despite decades of glass eel restocking, the implementation has not led to the expected population recovery. The reasons for this are unclear, but it could be that restocking results in a mismatch between genotype and habitat (Stacey et al., 2015). Hence, further understanding related to genetics and adaptive responses is urgently required.

Also our understanding on the effect of migration barriers on fish migration requires further research. The numerous migration barriers result in substantial delays of migratory fish species (Silva et al., 2018; Verhelst et al., 2018a,c). Although chances of disease, predation, fishing and therefore mortality may rise substantially, the effect of delays on the fitness and reproductive success of the animal is unknown. Such research has important implications for management. It would indicate that fish passage not only needs to be sufficient, it needs to be efficient as well.

Finally, Anguillid eels and diadromous species in general show some of the most extensive animal migrations known to man. These migrations are the result of long-term evolutionary trends and natural selection allowed the species to adapt and persist during the changing events of time. However, due to anthropogenic influences, the Earth's climate is changing faster than ever before leading to difficulties for species to adapt and, consequently, extinctions (Visser, 2008; Ceballos et al., 2015). Related to fish migration, climate change will likely lead to different hydrological conditions (Vörösmarty et al., 2000). This may not only result in the construction of migration barriers such as pumping stations, dams, weirs and hydropower plants, but also in conflicts between the migratory behaviour and the altered hydrological conditions. For instance, a dryer climate or higher anthropogenic water retention in reservoirs may lead to less run-off and consequently more limited migration windows.

Chapter 10

Addendum

10.1 Successful external acoustic tagging of twaite shad *Alosa fallax* (Lacépède 1803)

Modified after: Breine, J.; Pauwels, I.S.; Verhelst, P.; Vandamme, L.; Baeyens, R.; Reubens, J.; Coeck, J. 2017. Successful external acoustic tagging of twaite shad *Alosa fallax* (Lacépède 1803). *Fisheries Research* **191**: 36 - 40.

P. Verhelst contributed to the data collection, data analysis, generating the figures and writing the text.

10.1.1 Abstract

Although twaite shad declined substantially in many European rivers, its numbers increased since 2007 in the Belgian Zeeschelde. Since twaite shad is a

species of conservation concern, further knowledge on its migration and reproductive behaviour is needed and acoustic telemetry would be a relevant tool to assess these behaviours. Shads are very sensitive fish showing adverse reactions to handling and anesthesia, specifically twaite shad. Therefore, this species is rather unsuitable for internal implantation of electronic tags, such as acoustic, radio and data storage tags. Tests are needed to assess the impact of external tagging on twaite shad survival. Here we describe a fish friendly attachment procedure to externally tag the fish. The procedure is quick and may limit additional drag force on swimming as the tags are firmly attached to the body by a rubber plate. This procedure was developed in Belgium in spring 2015 to tag eight shads in the Zeeschelde. Five of these shads showed a migration pattern that generally corresponded with spawning activities observed visually in the river.

10.1.2 Introduction

Twaite shad is an iteroparous, anadromous clupeid occurring along the European coast from Morocco to the Baltic Sea, throughout the Mediterranean Sea and along the Northeastern Atlantic Coast (Aprahamian et al., 2003a; Maitland and Lyle, 2005). It is a marine pelagic fish species, but migrates during spring into the middle and upper reaches of the river to spawn (Maes et al., 2008).

Since the early nineties, a strong decline in twaite shad populations has been observed due to anthropogenic influences, such as water pollution, modification of river habitat and hydrology, and overfishing (Assis, 1990; Bervoets et al., 1990; Doherty et al., 2004). Following its decline, the species is classified

as vulnerable and listed under the International Union for the Conservation of Nature (IUCN) World Red Data Book (IUCN, 2015), included in Appendix III of the Bern Convention (CE, 1979) and Annexes II and V of the EC Habitats Directive (Aprahamian et al., 2003b). Despite a recent population increase in the Rivers Seine, Rhone, Ebro, Schelde, Elbe and Curonian Lagoon (Belliard et al., 2009; Lebel et al., 2001; López et al., 2007; Maes et al., 2008; Magath and Thiel, 2013; Stankus, 2009), the effect of the above described human impacts on twaite shad remains unsolved. Being an anadromous fish, the species is particularly vulnerable during the estuarine phase due to increased predation risk, diseases or the energetic cost of migrating and osmoregulatory abilities (Lochet et al., 2009). Hence, successful conservation and restoration of twaite shad populations requires insight into the effect of environmental conditions on spawning migration behaviour to aid successful reproduction.

Acoustic telemetry is a relative recent, but commonly applied technique to study fish behavior (Hussey et al., 2015). Fish are provided with an acoustic transmitter, which emits a signal with a unique ID code that can be detected by an ALS. This technique not only reveals the migration routes, but may also provide knowledge on the variables that influence migration and potential migration barriers when detection data, biotic and abiotic data are linked (Verhelst et al., 2018c). Surgical implantation is often used in tagging studies requiring pre- and post-operative care, anesthetics and confinement (Bridger and Booth, 2003; Huisman et al., 2016; Jepsen et al., 2005; Pauwels et al., 2014). Implantation has the potential to have both lethal and sublethal impacts on fish if performed incorrectly (Jepsen et al., 2002; Thiem et al., 2011). Due to the high sensitivity of twaite shad to handling and stress, surgical implantation could result in a high mortality and is therefore inadvisable. Rooney and

King (2014), for instance, stated that twaite shad exhibits an adverse reaction to handling and sedation and is therefore an unsuitable species for surgical implantation. Telemetry studies on allis (*A. alosa* Linnaeus 1758) and American (*A. sapidissima* Wilson 1811) shad have been conducted by means of gastric implantation of tags (Acolas et al., 2004; Dutterer et al., 2016; Frank et al., 2009; Olney et al., 2006; Tétard et al., 2016). Gastric implantation is a less invasive method than surgical implantation but it might result in regurgitation or mortality due to stomach rupture (Murphy and Willis, 1996; Nielsen, 1992). However, since twaite shad is more sensitive than allis and American shad (Baglinière and Elie, 2000), few telemetry studies have been conducted on twaite shad. Recently, Rooney et al. (2013) successfully applied external tagging on twaite shad in Ireland. Here, we present a protocol for external tagging of twaite shad, which is partly based on the method of (Rooney and King, 2014).

10.1.3 Material and methods

Study area

The River Schelde is 435 km long, originating on the plateau of Saint-Quentin in France. The Schelde estuary is approximately 160 km long and discharges into the North Sea. The estuary has a complete salinity gradient from polyhaline to a tidal freshwater zone, including extensive freshwater, brackish and salt marshes to its ecosystem (Fig. 10.1). It is a well-mixed estuary characterized by strong currents, high turbidity and a large tidal amplitude up to 6 m

(Seys et al., 1999). It can be divided in two sections (downstream to upstream): the Westerschelde (WS) in the Netherlands from Vlissingen to Zandvliet and the Zeeschelde (ZS) in Belgium, from Zandvliet to Gent. Further upstream the river is obstructed by sluices and weirs, which reduces tidal action and salt-water intrusion. Historical observations on the spawning sites of twaite shad in the River Schelde indicate they are located downstream of the first weir in the freshwater tidal reach of the watershed (Vrielynck et al., 2003). Therefore, in this study no physical migration barrier was encountered by the fish.

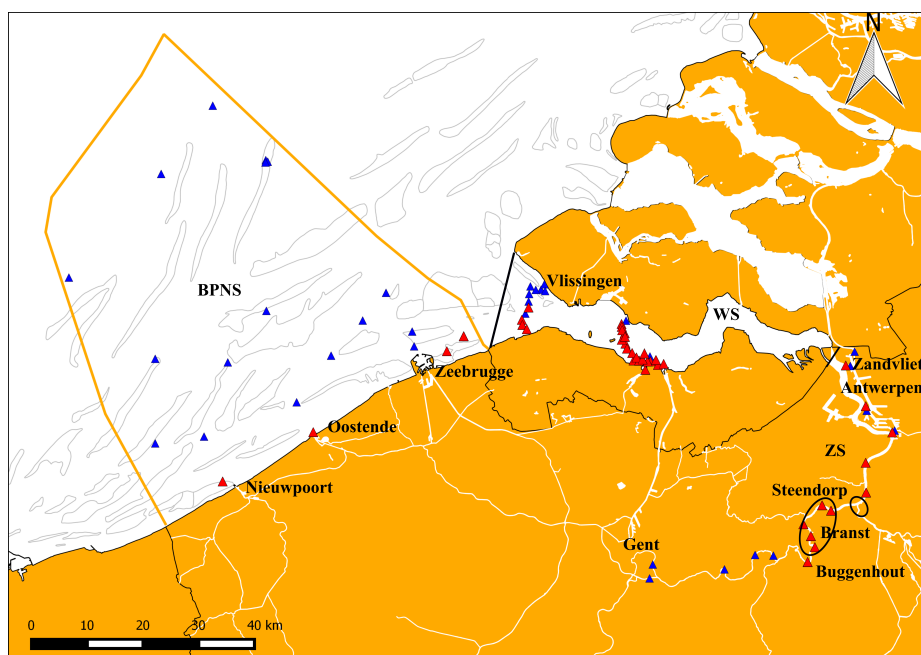


Figure 10.1: The locations of the acoustic listening stations (red triangles where shad were detected and blue triangles where shad were not detected) in the Belgian part of the North Sea (BPNS), Westerschelde (WS) and Zeeschelde (ZS). The borders between each of the three systems are indicated by a solid line. Spawning activity visually observed by people within a voluntary network, are indicated by circles.

ALS network

Within the framework of the LifeWatch observatory, a permanent acoustic network of 74 ALSs (VR2W, VEMCO Ltd, Canada) has been present since the spring of 2014 in the Zeeschelde (20 ALSs), Westerschelde (34 ALSs) and the

Belgian part of the North Sea (20 ALSs) (Section 2.3). They are moored at strategic locations to maximise the probability of detection. Hence, ALSs are deployed longitudinally in the Zeeschelde, in arrays in the Westerschelde and scattered in the BPNS (Fig. 10.1), thus covering around 180 km of river. The Belgian part of the North Sea stretches up to 81 km north and has a coastline of approximately 72 km long, covering a surface of 3454 km².

Tagging

Fish were caught in the Zeeschelde, near Antwerpen and Branst, with two mid-water beam trawls from an anchored boat in April 2015 (Breine et al., 2015). Each trawl consisted of a net fixed between two eight meter long steel beams. The lower beam was dropped to the bottom of the river while the upper beam was held at the surface. Both ends of the beams were attached to the anchor that keeps the boat at a fixed place. Two nets were submerged for one or two hours during flood and ebb tide, respectively. Fish caught in the nets remain unharmed as flood tide prevents the nets from collapsing. Landed shad were checked for external damage and general condition (i.e. the capture effect). For each fish, total length (to the nearest mm) and weight (to the nearest gram) were measured, whereafter they were transferred to a 50 L oxygenated tank. Eight twaite shads were tagged with coded acoustic transmitters (V7 and V9, VEMCO Ltd, Canada), which emit signals at 69 kHz (Table 10.1). The tags had the capacity to emit signals for 2 (V7) and 4 (V9) months. The weight of the tags never exceeded 2% of the body mass of the captured shads (Jepsen et al., 2005).

To tag the captured fish, they were transferred to a surgery basin filled with

Table 10.1: Used tag types and properties.

Transmitter type	Number of shads tagged	Length (mm)	Diameter (mm)	Weight in air (g)	Weight in water (g)	Battery life (days)
V7	4	18	7	1.4	0.7	64
V9	4	24	9	3.6	2.2	132

sufficient aerated water to cover the head whilst exposing the dorsal surface. Fish were held partly under water with the head covered by a wet towel during the tagging procedure. Two to three scales were removed under the dorsal fin with a medical forceps to allow easy perforation of the two hollow needles (20G). A surgical thread (Ethilon) attached to the tag by a heat-shrinkable sleeve was passed through each needle so that they pass through the body of the fish while withdrawing the needles. A two mm thick rubber plate attached to the needles was then slid over the threads to reduce friction from the tag. Finally, the tag was drawn tightly against the dorsal fin and the plate was stabilized with two aluminum sleeves (Fig. 10.2). After tagging, the fish were placed back in the oxygenated tank for approximately 30 seconds until they started swimming. Then they were released into the Zeeschelde at their catch location. An overview of the tagging protocol is given in Table 10.2. Handling never took more than 90 seconds and could be reduced to this minimum by not anesthetizing the fish. The experiment was approved by the Ethical Committee of the Research Institute for Nature and Forest in Brussels (LA 1400559) and complies with the national legislation in Belgium transposing EU Directive 2010/63/EU (2010) on the protection of animals used for scientific purposes.



Figure 10.2: Dorsal view of fixed tag under the dorsal fin.

10.1.4 Results and discussion

In this study, we present a method for external tagging of twaite shad, adapted from a protocol described by Rooney and King (2014). The main difference with the method of Rooney and King (2014) was the attachment of the tag to the body to reduce friction. In Rooney and King (2014), the tag could freely move, which may enhance the chance of irritation. However, our results were similar to Rooney and King (2014) and in both studies, no recapture of tagged individuals occurred that would allow to draw conclusions about potential skin irritation due to tagging. Nonetheless, based on the telemetry results, twaite shads may not be strongly affected by the tags during the tracking period. In

Table 10.2: Procedure external tagging of twaite shad.

Preparation	<ol style="list-style-type: none"> 1. Necessary material <ul style="list-style-type: none"> • Tag • Surgical thread (Ethilon) • Two hollow needles (20G) • Heat-shrinkable sleeve and aluminium sleeves • Rubber plate (2 mm) • Aerated tanks for surgery and recovery • Medical forceps 2. Prepare the tags by attaching a 20 cm long Ethylon thread to the tag with the heat-shrinkable sleeve. Each thread-end should later be passed through one of the two hollow needles that perforate the shad's dorsal fin.
Transfer caught fish	<ul style="list-style-type: none"> • Place shad in aerated tank and check its condition. • Evaluate the tag/fish weight ratio. • Transfer the shad to the surgery basin.
Position caught fish	<ul style="list-style-type: none"> • Position the fish with the dorsal fin upwards and above the water • Gently cover the head with a wet towel to reduce handling stress
Performing the surgery	<ul style="list-style-type: none"> • Remove two to three scales below the dorsal fin with a medical forceps. • Perforate the rubber plate with the two hollow needles. • Perforate the shad with two hollow needles just below its dorsal fin where the scales were removed. • Pass the surgical Ethilon thread through the hollow needles (one thread per needle) and pull the tag against the shad's body. • Slide the rubber plate over the thread to the shad's body. • Stabilize the rubber plate with two aluminum sleeves.
Transfer tagged fish	<ul style="list-style-type: none"> • Transfer the tagged shad back to the aerated tank to evaluate its welfare for approximately 30 seconds. • Release the tagged shad at the catch location.

total, 22 adult twaite shads (mean total length 39.7 cm, range: 33.9-47.3 cm) were caught during upstream spawning migration in the Zeeschelde near Antwerpen and Branst (Fig. 10.1). Two of these shads were injured after landing. Probably they got wounded by debris carried by the currents into the nets.

Eight of all caught twaite shads were acoustically tagged. One of these eight shads was never detected at a listening station, while two were detected at only one location for less than a day and 31 days, respectively. A plausible explanation would be that the tag was detached or the fish died, either as a result of the tagging procedure or by predation. Predation by cormorants (*Phalacrocorax carbo* Brisson, 1760), for instance, can certainly not be ruled out.

The remaining five tagged shads were detected at on average 21 ALSs (range 8-30 ALSs), and all together they were detected at 39 out of 74 ALSs between April 22th 2015 and June 28th 2015 (Table 10.3). Note that the tracking period varied among shad and lasted between 23 and 65 days. Specifically, the most upstream detection location was about 110 km upstream of the mouth of the estuary and the furthest detection location in the BPNS was near the coast-line in Nieuwpoort, about 135 km from the catch location of the shad. Further, all five shad showed both upstream and downstream movement behaviour. The extent of their movements was similar to the study of Rooney et al. (2013), who found six of out eight shad that provided extensive tracking data. In the Zeeschelde, in 2015, twaite shad spawned in the tidal freshwater part between Buggenhout and Steendorp (90 km upstream) (visual observations).

We chose not to use anesthesia to reduce handling time, as this might be a crucial aspect to improve twaite shad survival. Notably, the effectiveness of a certain dose of anesthesia can vary according to the water temperature (Jepsen et al., 2002). Although Hao et al. (2006) and Ross et al. (1993) indicated a positive effect of anesthesia on American shad, we hypothesized that the recovery time from anesthesia of 6 to 7 minutes (Ross et al., 1993) would prolong the procedure too much, thus increasing the chance of death after release of the

twaite shad (de Laak, 2009). The absence of anesthetics in the external tagging procedure of salmon (Thorstad et al., 2000) and the gastric implantation of tags in other shad species (e.g. Bailey et al. (2004) for American shad and Tétard et al. (2016) for Allis shad) might further support this. Nonetheless, the potential positive effect of anesthesia on twaite shad handling stress should be further investigated (Hao et al., 2006; Ross et al., 1993).

Table 10.3: Number of tagged twaite shad with tag type, total length (cm), weight (g), catch location and date, first and last detection, tracked time (days), number of locations and different areas where the fish were detected (Belgian part of the North Sea (BPNS), Westerschelde (WS) and Zeeschelde (ZS)).

Length (cm)	Weight (g)	Catch location	Catch date	First detection	Last detection	Tracked time (days)	Acoustic Listening Stations (ALSs)	Areas
35.2	378	Antwerp	23 rd April	24 th April	17 th May	23	8	ZS - WS
37	456	Antwerp	23 rd April	24 th April	28 th June	65	30	ZS - WS - BPNS
34.5	360	Branst	22 nd April	22 nd April	17 th May	25	21	ZS - WS
45.6	822.4	Branst	22 nd April	22 nd April	17 th May	25	22	ZS - WS
33.9	325	Branst	22 nd April	22 nd April	22 nd May	30	26	ZS - WS - BPNS
35.3	365.6	Branst	22 nd April	23 rd April	17 th May	0	1	ZS
40.5	591.1	Branst	22 nd April	NA	NA	0	0	NA
44	800	Branst	30 th April	30 th May	31 st May	31	1	ZS

10.1.5 Conclusion

The new external tagging technique is promising as it did not prevent tagged shads from extensive up- and downstream migrations in the Schelde estuary and the BPNS for a period up to two months. Since tagged shads were not recaptured, it is unknown to what extent external tags could affect the fish's physiology and movement behaviour. Therefore, further research can help to understand the direct effects on the shad's welfare, so that the method can be further improved and applied to other *Alosa* species as well. In this respect, further research on the effect and doses of anesthesia, and of handling and tagging twaite shads is strongly encouraged. Tagging more individuals, accompanied by laboratory monitoring of tagged fish, could reveal important information about movement behaviour, tag loss, lesions and infections. Telemetry studies on a larger number of twaite shad are important, because they can provide essential information on the shad's spatio-temporal behaviour, which may well be important for the establishment of successful species management and conservation plans.

Chapter 11

Supplemental information

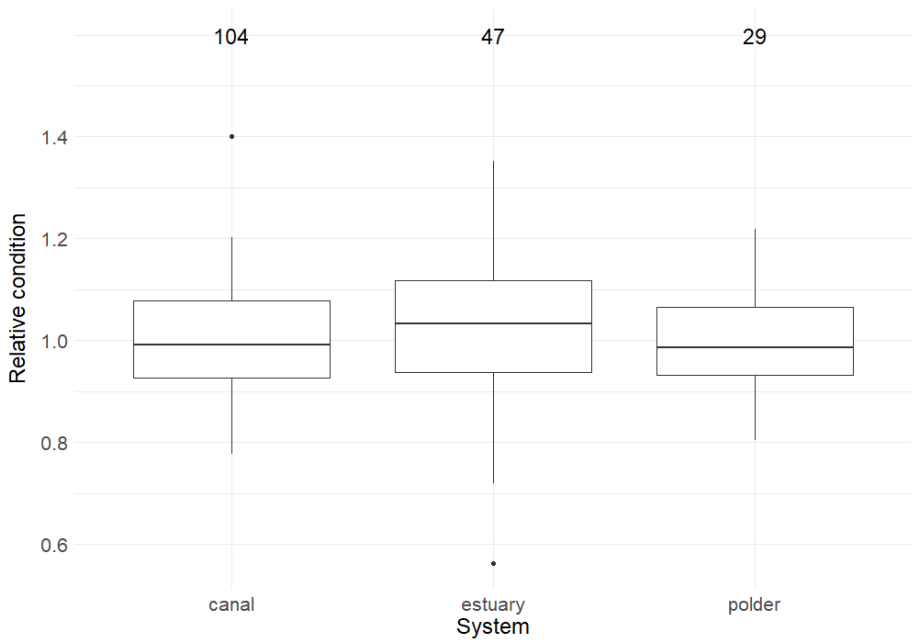


Figure S1: The relative condition factor (Kn) did not differ significantly between silver eels (FV) from the polder, estuary and Albert Canal (one-way ANOVA, $F(2,177) = 0.062$, $p = 0.94$).

Chapter 12

Curriculum vitae

Academic education

- 2008 – 2011: Ghent University, Bachelor in Biology (cum laude)
- 2011 – 2013: Ghent University, Master in Biology (magna cum laude)

Academic experience

- 1 May – 30 September 2014: researcher UGhent (Faculty of Bioscience engineering, Applied Ecology and environmental Biology department)
- 1 October 2014 – present: PhD student UGhent (Faculty of Science, Marine Biology department)

Peer reviewed A1-publications

1. Breine, J., Pauwels, I.S., **Verhelst, P.**, Vandamme, L., Baeyens, R., Reubens, J., Coeck, J. 2017. Successful external acoustic tagging of twaite shad *Alosa fallax* (Lacépède 1803). *Fisheries Research* **191**: 36 - 40.
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*Joint first authorship
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 10. **Verhelst, P.**, De Meyer, J., Reubens, J., Coeck, J., Goethals, P., Moens, T., Mouton, A. Unimodal head width distribution in wild European eel (*Anguilla anguilla* L.). *PeerJ* **6**: e5773.
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4. **Verhelst, P.** 2015. Fish 'n chips. *Hét Hengelblad*, jaargang 24, nr. 1: 23 – 25.
5. **Verhelst, P.** 2016. Paling in 't groene Meetjesland. *Natuur en Landschap Meetjesland*, jaar 2016, nr. 3: 10 – 11.

6. **Verhelst, P.** 2017. Noord, Zuid of maakt het niet uit? *HengelSport*, jaargang 26, nr. 2: 40 – 45.
7. **Verhelst, P.** 2017. Shortcuts in de reis van de paling. *Visionair*, jaargang 11, nr. 43: 22 – 24.

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1. Breine, J., Van den Bergh, E., Pauwels, I., **Verhelst, P.**, Coeck, J. (2016). The return of the twaite shad in the Zeeschelde. ECSA Local Meeting 2016. Antwerp, Belgium. 1 poster pp.
2. **Verhelst, P.**, Huisman, J., Reubens, J., Goethals, P.L.M., Moens, T., Mouton, A.M. 2016. Marine migration routes of North-western European silver eel (*Anguilla anguilla* L.). Fish Passage 2015, Groningen, The Netherlands. 1 poster pp.
3. **Verhelst, P.**, Huisman, J., Reubens, J., Goethals, P.L.M., Moens, T., Mouton, A.M. 2015. Marine migration routes of North-western European silver eel (*Anguilla anguilla* L.). Startersdag in natuur en bosonderzoek 2015, Brussels, Belgium. 1 poster pp.
4. **Verhelst, P.**, Huisman, J., Reubens, J., Goethals, P.L.M., Moens, T., Mouton, A.M. 2015. Marine migration routes of North-western European silver eel (*Anguilla anguilla* L.). International Conference of Fish Telemetry 2015, Halifax, Canada. 1 poster pp.
5. **Verhelst, P.**, Huisman, J., Reubens, J., Goethals, P.L.M., Moens, T., Mouton, A.M. 2016. Marine migration routes of North-western European silver eel (*Anguilla anguilla* L.). VLIZ Marine Science Day 12 February 2016. Marine Biology, Ghent University: Gent. 1 poster

pp.

6. **Verhelst, P.**, Bridger, S., Rappé, K., Reubens, J., Goethals, P., Mouton, A., Moens, T. 2016. Conversation to conservation for the European eel (*Anguilla anguilla* L.) management. CommOcean 2016, Bruges, Belgium. 1 poster pp.
7. **Verhelst, P.**, Buysse, D., Reubens, J., Pauwels, I., Aelterman, B., Van Hoey, S., Goethals, P., Moens, T., Coeck, J., Mouton, A. 2017. Emigration of European eel (*Anguilla anguilla* L.) from a polder system into the Schelde estuary. International Eel Science Symposium 2017, London, UK. 1 poster pp.

Oral presentations

1. **Verhelst, P.** 2016. Gebruik van akoestische telemetrie bij populatiebeheer van vissen. Vissennetwerk, Bornem, Belgium.
2. **Verhelst, P.**, Bruneel, S., Reubens, J., Coeck, J., Goethals, P., Oldoni, D., Mouton, A., Moens, T. 2018. Selectief getijdetransport bij stroomafwaarts migrerende palingen (*Anguilla anguilla* L.) - Migratiegedrag in een dynamisch estuarium. Scheldesymposium 2018, Antwerp, Belgium.
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 9. **Verhelst, P.**, Reubens, J., Aeltermann, B., Buysse, D., Coeck, J., Goethals, P., Moens, T., Mouton, A. 2016. Estuarine behaviour of European silver eel (*Anguilla anguilla*). International Symposium on Ecohydraulics 2016, Melbourne, Australia.
 10. **Verhelst, P.**, Reubens, J., Aeltermann, B., Buysse, D., Coeck, J.,

- Goethals, P., Moens, T., Mouton, A. 2016. Migratie van Europese zilverpaling (*Anguilla anguilla*) in een door de mens beïnvloed poldergebied. Startersdag in natuur en bosonderzoek 2016, Brussels, Belgium.
11. **Verhelst, P.**, Pauwels, I. 2016. Gebruik van akoestische telemetrie bij populatiebeheer van vissen. Waterforum, Ghent, Belgium.
 12. **Verhelst, P.**, Reubens, J., Moens, T., Mouton, A.M. 2015. Estuarine behaviour of European silver eel (*Anguilla anguilla*) in the Scheldt Estuary: a slippery path. VLIZ Young Scientist Day. Bruges, Belgium, 20 February 2015.
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Awards

- Best oral presentation at 'Startersdag in natuur en bosonderzoek 2016', Brussels, Belgium.
- Communication Award at 'VLIZ Marine Science Day 2016', Bruges, Belgium.

Student guidance

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- Thomas Lanssens (Msc Biology) (as supervisor)
- Toon Saerens (Msc Biology) (as supervisor)

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